AN EXPERIMENTAL STUDY OF THE WATER RELATIONS OF SEEDLING CONIFERS WITH SPECIAL REFERENCE TO WILTING

ROBERT MARSHALL

SUBMITTED TO THE BOARD OF UNIVERSITY
STUDIES OF THE JOHNS HOPKINS UNIVERSITY
IN CONFORMITY WITH THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

BALTIMORE, MARYLAND
1930

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AN EXPERIMENTAL STUDY OF THE WATER RELATIONS OF SEEDLING CONIFERS WITH SPECIAL REFERENCE TO WILTING*

INTRODUCTION

The present paper reports the results of a limited study on the physiological ecology of conifer seedlings. The study was undertaken as a piece of physiological research with an ecological viewpoint, but the species of plants used and the general plan followed will perhaps make it of value to those who are interested in forest ecology, as the results reported deal with the water relations between plant health and soil-moisture conditions for some representative conifers during the seedling stage.

Many investigators have taken part in developing present day knowledge of plant wilting as related to soil-moisture conditions. Sachs ('59) allowed tobacco plants to wilt in soils of different texture and showed clearly that the amount of water remaining in the soil at the time of wilting was related to the size of the soil particles; the coarser the soil, the smaller the amount of water left. At about the beginning of the present century Heinrich ('94), Gain ('95), Hedgcock ('02) and Clements ('05) measured the amount of water remaining in the soil when plants of several different kinds had wilted, and concluded that drought resistance might be estimated in terms of the soil-moisture content when wilting occurs. Many investigators have studied this so-called non-available water content, which Clements has called the echard. Briggs and Shantz ('11, '12, '13) carried out an extensive series of experiments which have greatly influenced subsequent progress of knowledge along these lines. They presented more data than had ever been available before and improved technical methods. They studied twenty different types of soil, more than a hundred species of plants, and made in all more than 1,300 separate determinations of soil-moisture corresponding to what they termed permanent wilting of the plants. On the basis of the ideas introduced by these writers, and with due reference to further developments by other students of water relations, permanent wilting may be defined as that stage in the progressive wilting of a plant at which the rate of water absorption through the roots becomes so slow that, even though there is no further water loss through transpiration, recovery of turgor is impossible without increasing the water content of the soil. Thus the amount of water left in the soil at the beginning of permanent wilting becomes a serviceable measure of what the earlier writers termed non-available soil moisture. Briggs and Shantz came to the somewhat startling conclusion that all plants were capable

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of drying a given soil to practically the same extent, being thus in pronounced disagreement with most earlier experimenters, who had thought that species differed with respect to their capacity for removing water from the soil. It is true that Cameron and Gallagher ('08) had previously suggested a similar generalization. Briggs and Shantz found, however, that the amount of water left in the soil at the beginning of permanent wilting differed greatly for different soils, and concluded that it was directly related to the moisture equivalent. This soil characteristic, as defined by Briggs and McLane ('07), is the residual water retained by the soil after it has been subjected under standard conditions to a centrifugal force equivalent to 1,000 times gravity. Because of an apparently constant relationship between the moisture equivalent of the soil and the amount of water remaining at the beginning of permanent wilting in their experiments, Briggs and Shantz presented formulas to give what they called the wilting coefficient of the soil, which was thus regarded as a soil characteristic.

Several subsequent writers have questioned the conclusion that the nature of the plant has no bearing on the soil-moisture content at the beginning of permanent wilting. Crump ('13) attributed these results of Briggs and Shantz to the prevalence of agricultural crops among the material with which they worked, to the particular conditions of their experiments (especially the low transpiration rates prevailing), and to the difficulty of determining just when permanent wilting sets in. Wilson's studies ('27) indicated that different kinds of plants may enter permanent wilting with markedly different soil-moisture residues. Maximov ('29), on the other hand, seems to consider the preponderance of evidence as in agreement with Briggs and Shantz. Brown ('12), Caldwell ('13), and Shive and Livingston ('14) all presented evidence indicating that the residual moisture in the soil at the time of wilting varied not only with the soil texture but also with the atmospheric environment, the greater the evaporating power of the air the greater the moisture content of the soil when the plants entered permanent wilting. Recent studies of Veihmeyer ('27) and Veihmeyer and Hendrickson ('27, '28) seem to support the earlier conclusions of Briggs and Shantz in this regard. Several investigators, notably Brown ('12) and Thom and Holtz ('17), pointed out that the conditions under which plants had been grown has also influenced the amount of residual soil moisture at the onset of permanent wilting. Plants grown in moist soil left more water in the soil when water absorption practically ceased than was left by plants grown in drier soil. Harris ('14) and Jean and Weaver ('24) observed that "the general effect of decreased water content of the soil, providing enough is available to produce moderate growth, is to accelerate root development in relation to growth of tops."

It is apparent that general agreement has not been reached with respect to this vexed question of the relation of wilting to soil-moisture content. A sort of dynamic approach to this important question was suggested even be-

fore the time of Briggs and Shantz's work, when Livingston ('06) used Pfeffer osmotic cells as standard water absorbers (like artificial roots). The same writer presented some observations on the capacity of a soil to deliver water to the supernatant air through ordinary evaporation. The osmometer method for studying soil-moisture conditions was later improved by Pulling and Livingston ('15) and by Pulling ('17), but it did not appear to be very promising. Dry porous porcelain was introduced as a water absorber by Livingston and Koketsu ('20), who first employed the porcelain cones called soil points. These, like the osmotic cells mentioned above, imitate plant roots in that they remove water rapidly from the soil in which they are placed. With some improvements, soil points have been used by Thone ('22), Livingston and Ohga ('26), Livingston, Hemmi, and Wilson ('26), Wilson ('27), Baldwin ('28) and others. Using the same general principles, and at Livingston's suggestion, Mason ('22) and Hardy ('23, '24) employed as water absorbers ordinary lead pencils sharpened to uniform conical points by means of a mechanical sharpener. These experimenters were no longer studying the static water content of the soil and its fluctuations. They turned attention to the dynamic water-supplying power of the soil—in other words, the rate at which water was available to the absorbing surface of the plant. The aim of those employing the soil-point method has been similar to that for the attainment of which osmometers had been tried; namely, to measure the capacity of the soil to deliver water to a suitable standard water-absorbing surface. The soil-point method will be considered in some detail further on. It at least offers great promise for dynamic soil-moisture studies. It permits the comparison of soil-moisture-supplying power with the water-absorbing power of the plant and with the plant's turgor or stage of wilting, and it makes such comparisons possible without any reference to the coarseness or fineness of the soil or its state of packing. Soil-point readings at the onset of permanent wilting have been found to be the same, or very nearly the same, for soils of different degrees of fineness, at least when the same kind of plant in the same developmental stage and with the same climatic complex is employed for the tests.

As has been suggested, one great difficulty has always beset students of plant wilting, that of ascertaining just when a plant is wilted to any specified degree. Wilting is, of course, a progressive process and cannot be sharply separated into distinct phases, but, following Livingston ('17), four stages may be outlined as follows: (1) Incipient drying—the usual fluctuating water deficit due to tissue water contents somewhat below the water content at maximum turgor. (2) Temporary wilting—a continuous series or range of wilting stages from which the wilted tissues may recover if transpiration is subsequently decreased and remains low for a sufficient time. (3) Permanent wilting—the series of stages from which plants cannot recover unless the rate of water supply to the roots is increased. (If permanent wilting proceeds far enough death supervenes.) (4) Post-mortem desiccation. The

onset of any specific stage of progressive wilting is in most instances, very difficult to ascertain by eye. It is only rarely that the experimenter has as satisfactory material as Koketsu's ('25) Mimosa. In tender herbaceous plants it is in many cases possible to observe ocularly the beginning of temporary wilting and the onset of some subsequent stages. When it comes to such plants as conifers or cacti, however, it is almost or quite impossible to decide by direct observation just when any stage of wilting has begun. Briggs and Shantz ('12) suggested that permanent wilting in a cactus might be considered as beginning when the plant had lost 1 per cent of its original water content. Different tissues of any wilting plant do not lose in water content at the same relative rates, however. As Livingston ('12) has pointed out, many of the leaves of a plant may have dried enough to be killed while some other parts may still be highly turgid and even growing. MacDougall, Long and Brown's ('15) Echinacactus that received no external water for several years had lost a large part of its original water but it persisted in producing flowers and fruits at the usual season. Nevertheless, the suggestion of Briggs and Shantz leads to the thought that different degrees or stages of decreased turgor or of progressive wilting might be identified in terms of the relative water contents of the tissues considered.

Many observers have found that plant water content fluctuates remarkably, even in a single day. Livingston and Brown ('12) specifically pointed out that the diurnal minimum of foliar water content furnished a criterion by which the approach of the beginning of temporary wilting might be detected. In Bakke's ('15, '18) experiments on the diminishing transpiring power of wilting leaves he found that the beginning of permanent wilting appeared to correspond to a temporary increase in transpiring power. He measured transpiring power by the method of the standardized hygrometric paper devised by Livingston ('13) and improved by Livingston and Edith B. Shreve ('16). Koketsu ('26) studied the progress of wilting with reference to changes in the transpiration rate. He says: "During the process of wilting the index of the transpiring power itself decreases progressively until it reaches its minimal value at the critical point of wilting. After that time, it begins again to rise more or less, and then the plant falls into the drying phase of low transpiration or evaporation."

The foregoing paragraphs are not intended to be a review of the extensive literature of the soil-moisture relations of plants. They may serve, however, to illustrate some of the main considerations from which further research needs to start. In the present study of wilting and drying in young conifer seedlings, the changing appearance of the seedlings was observed and their diminishing water content was measured. An ocular criterion of the beginning of permanent wilting was employed, but it was unsatisfactory and water content appeared to furnish a more definite criterion. The water-supplying power of the soil at the time the seedlings entered a rather definite stage of wilting was ascertained.

The experiments described in this paper were carried on at the Laboratory of Plant Physiology of the Johns Hopkins University, where equipment and facilities were freely furnished. The author wishes to acknowledge indebtedness to the pioneer publications by Bates and Zon ('22), Bates ('23), and Pearson ('24). Especially he wishes to express his appreciation for very essential advice, guidance, and criticism received from Professor Burton E. Livingston, Director of the John Hopkins Laboratory of Plant Physiology.

Experiments

The seedlings.—The seedlings for this study had been grown from seed in rectangular boxes of soil in a greenhouse room. These boxes were of galvanized sheet iron, 30 cm. wide, 55 cm. long and 20 cm. deep. The soil mass was about 15 cm. deep in each box, including a bottom layer of cinders 2 cm. deep. Only one kind of seed was planted in any box. The soil was kept moist by frequent watering throughout the period between planting and the beginning of an experiment, which occurred about 24 days after the appearance of the plantlets above the soil surface. The whole period from the time of planting covered 34 to 60 days, varying with the time required for germination. Some species appeared above the soil in only 10 days; others, after more than a month. Throughout the period of watering the water-supplying power of the soil at a depth of from 3 to 5 cm. generally fluctuated roughly between 150 and 250 mg. for the first hour of absorption, as read on Livingston soil points. This corresponded to a volumetric water content between about 5.2 and about 7.1 per cent. At the end of the preparatory period watering was discontinued and observations on water content of tops were immediately begun and continued throughout the subsequent drying period.

The soil used was a nearly pure, white quartz sand with a water-holding power of 36.4 per cent on a volumetric basis, or 26.0 per cent on the basis of dry weight. These values were secured by means of the Hilgard ('12) method with a 1-cm. column of soil. Oven-dry, without packing, this sand weighed 1.95 g. per cubic centimeter.

As a guide in the placing of the seeds on the leveled soil surface a piece of galvanized wire netting with square meshes about 8 mm. in diameter was laid on the soil and one seed was placed in the center of each opening. The seeds were thus regularly spaced about 8 mm. apart in each direction, 1,500 seeds being uniformly distributed over the seed bed, which was 30 cm. wide and 55 cm. long. After being placed the seeds were covered with sand, regularly to a depth of 7 mm. but to a depth of 10 mm. for the unusually large seeds of western yellow pine and slash pine. A suitable wooden block supported on the opposite margins of the box and easily slid from one end of the seed bed to the other was used as a gauge to smooth the soil at the proper level before the seeds were planted and another block was used similarly after the sand cover had been applied.

The twelve species of coniferous trees studied are listed in Table I. Nine experiments were performed with Norway spruce, 6 with Norway pine and 1 with each of the other species. The necessary supplies of seed were kindly furnished by the United States Forest Service, the New York State Conservation Commission, and the Louisiana Department of Conservation. The writer is gratefully appreciative of the kindness of Raphael Zon, Julius F. Kümmel, D. S. Olsen, E. L. Demmon, L. J. Pessin and W. G. Howard, who helped in procuring seeds. Some special data concerning the lots of seed used are given in Table I.

In order that all seedlings used in an experiment should have developed under similar conditions and should be of nearly the same age, measured from the time of their appearance above the soil, seedlings that germinated early or late were removed from the beds before the beginning of an experiment and those used were all of nearly the same age, from about 21 to 27 days. The range of ages in any one experiment was usually only 7 days, although, with a few beds it was necessary to allow this range to be as much as 13 days. Ages (from the time of appearance above the soil) are shown by the dates given in Table II, along with average stem height and root length for the beginning of each experiment. Very uniform stands of seedlings

TABLE I. *Seed data.*

Species	Year of Crop	Source	Altitude of source above sea level	Average weight per seed	Times of planting
			Feet	*Mg.*	
Abies grandis Lindl. (Lowland white fir)	1929	Montana	3,000	18.9	Jan., 1930.
Picea excelsa (Norway spruce)	1928	Norway	.....	7.4	Mar., Oct., Nov., 1929; Jan., Feb., 1930.
Picea glauca B. S. P. (White spruce)	1928	Ontario	.....	3.7	Mar., Oct., 1929.
Pinus caribaea Morelet. (Slash pine)	1928	Georgia	.....	28.0	Oct., 1929.
Pinus echinata Mill (Shortleaf pine)	1928	Louisiana	.....	9.1	Oct., 1929.
Pinus monticola D. Den. (Western white pine)	1929	Idaho	3,000	14.6	Dec., 1929.
Pinus ponderosa Laws. (Western yellow pine)	1927	Montana	4,500	52.2	Oct., 1929.
Pinus resinosa Sil. (Norway or red pine)	1927	Wisconsin	.....	6.3	Mar., Oct., Nov., 1929; Jan., 1930.
Pseudotsuga taxifolia Britt. (Douglas fir)	1928	Washington	500	12.5	Oct., 1929.
Thuja occidentalis L. (Northern white cedar)	1928	New York	.....	1.2	Mar., Oct., 1929.
Thuja plicata D. Don. (Western red cedar)	1929	Montana	3,000	0.9	Jan., 1930.
Tsuga heterophylla Sarg. (Western hemlock)	1929	Idaho	2,500	0.8	Jan., 1930

TABLE II. *Dates of experiments and heights of plants when experiments began; that is, when watering was discontinued.*

Species	Exp. No.	Average Date of first Appearance above soil	Beginning of Experiment	Stem Height	Root Length	Occurrence of critical wilting	End of Experiment
				Cm.	*Cm.*		
	1	May 3, '29	May 27, '29	4.0	2.3	June 3, '29	June 4, '29
	2	Nov. 8	Dec. 4	3.3	4.2	Dec. 9	Dec. 22
	3	Dec. 15	Jan. 12, '30	3.9	3.8	Jan. 17, '30	Jan. 25, '30
	4	Dec. 15	Jan. 12	3.7	3.5	Jan. 18	Jan. 25
Norway spruce	5	Jan. 23, '30	Feb. 20	3.2	4.8	Feb. 23	Feb. 28
	6	Feb. 23	Mar. 20	3.0	4.0	Mar. 24	Mar. 31
	7	Dec. 15, '29	Feb. 13	3.8	5.8	Feb. 18	Feb. 27
	8	Nov. 8	Jan. 15	3.3	6.0	Jan. 22	Jan. 23
	9	Nov. 8	Feb. 13	3.4	8.6	Feb. 22	Mar. 4
	10	Nov. 12	Dec. 6, '29	3.4	4.1	Dec. 14, '29	Dec. 22, '29
	11	Dec. 20	Jan. 15, '30	3.3	3.7	Jan. 23, '30	Feb. 4, '30
Norway pine	12	Dec. 20	Jan. 15	3.4	3.8	Jan. 24	Feb. 4
	13	Jan. 27, '30	Feb. 23	3.2	4.9	Feb. 28	Mar. 4
	14	Dec. 20, '29	Feb. 13	3.5	6.2	Feb. 24	Feb. 28
White spruce	15	Nov. 15	Dec. 10, '29	3.3	3.4	Dec. 15, '29	Dec. 21, '29
Northern white cedar	16	Nov. 17	Dec. 12	1.9	2.8	Dec. 18	Dec. 20
Shortleaf pine	17	Nov. 14	Dec. 9	2.8	5.1	Dec. 18	Dec. 18
Slash pine	18	Nov. 15	Dec. 10	5.0	6.3	Dec. 18	Dec. 18
Western yellow pine	19	Nov. 18	Dec. 12	3.4	7.0	Dec. 19	Dec. 21
Western white pine	20	Jan. 18, '30	Feb. 13, '30	3.7	7.0	Feb. 21, '30	Feb. 21, '30
Douglas fir	21	Nov. 22, '29	Dec. 15, '29	3.1	5.4	Dec. 21, '29	Dec. 22, '29
Lowland white fir	22	Feb. 3, '30	Mar. 1, '30	3.5	5.4	Mar. 7, '30	Mar. 13, '30
Western red cedar	23	Jan. 25	Feb. 20	1.7	4.3	Feb. 25	Feb. 28
Western hemlock	24	Feb. 11	Mar. 7	1.6	1.4	Mar. 11	Mar. 13

were usually secured by this method. Whenever the seedlings of a sample were removed from a bed for the determination of the water content of tops they were selected by eye to be representative of the entire stand and the few seedlings in any stand that were unusually large or small were not used in the samples. Heights were measured from junction of root and stem to insertion of cotyledons. In Table II the dates of the first appearance of the seedlings above the soil, are shown for each experiment the dates of beginning and end of the experiment, and the date of critical wilting.

Atmospheric Conditions and Radiation during Experiment Periods.—The atmospheric conditions of the experiments differed more or less. Continuous records of air temperatures were obtained from a shaded thermograph. Daily atmometric records were made from two standardized white porous-porcelain atmometers, corrected to the Livingston ('15) standard for white spheres, the readings being taken at 9 o'clock each morning. The drying effect of radiation was approximated for each day by means of a Livingston radio-atmometer ('11), consisting of two atmometer spheres operated side by side, one white and the other blackened with a collodion-lampblack film (Livingston and Wilson, '26). The index of radiation effect is taken as the difference between the corresponding corrected readings from the two spheres. The climatic records are summarized in Table III. They may be useful as showing at least some important features of the climatic influences that prevailed during the experiment periods.

Measurement of Water Contents of Seedling Tops.—The moisture contents of representative seedlings, excluding the roots, were measured at the beginning of each experiment and at frequent intervals thereafter until a critical moisture-content value had been passed, and in many cases until the seedlings were dead and nearly air dry. These measurements were made by sampling. For each sample 10 representative seedlings were taken from the bed, their roots were removed and the remaining top portions were then placed in a closed chamber, from which they were transferred one at a time for the first weighings. After each individual had been weighed it was placed upright in a carrying rack; a horizontal perforated disc of sheet metal supported on an evaporating dish. The tiny stems were inserted from above, one in each perforation, with the leaves resting on the disc. Each sample had its own rack. The use of the racks made it easy to keep the several individuals of a sample separate, without risk of interlocking of the needles. After the first weighings had been made any tops that deviated in weight from the average of the ten by more than 25 per cent were discarded. Not more than three were thus thrown out as irregular in any case and the whole 10 were usually retained. The average green weight per top for the "corrected" sample was taken to represent the average green weight of the tops of the whole population of the bed from which the sample had been taken. The general consistency of the results indicates that this method of

TABLE III. *Records of climatic conditions in the greenhouse during the experiments.*

Date	Maximum shade temperature	Minimum shade temperature	Atmometer loss (white sphere)	Atmometric index of solar radiation
	Deg., F.	*Deg., F.*	*Ml.*	*Ml.*
May 2, '29	..	..	3	0.5
3	..	..	12	0.5
4	..	..	15	1.0
5	..	..	7	1.4
6	..	..	12	1.1
7	..	..	16	1.8
8	..	..	14	1.1
9	..	..	10	1.2
10	..	..	18	1.8
11	..	..	16	1.8
12	..	..	16	1.8
13	..	..	6	0.3
14	..	..	4	1.0
15	81	60	16	1.5
16	83	58	19	1.7
17	76	50	13	1.7
18	76	53	11	1.4
19	82	65	10	1.2
20	69	51	2	0.4
21	66	50	7	0.9
22	78	50	24	2.6
23	78	49		
24	80	55	12	1.8
25	84	57	15	1.1
26	81	56	12	1.7
27	78	61	9	0.9
28	89	64	8	1.1
29	81	65	5	1.0
30	86	63	11	1.4
31	96	64	15	1.6
June 1	91	64	21	1.2
2	80	56	16	0.9
3	..	..	12	0.7
4	..	..	15	1.6
5	..	..	13	1.3
6	83	57	12	1.0
7	90	66	17	1.1
8	70	56	4	0.0
9	71	54	11	1.4
10	75	56	15	1.7
11	89	52	..	...
Nov. 8	77	..	13	0.3
9	85	62	24	2.4
10	80	55	16	1.5
11	81	63	20	2.0
12	82	64	13	0.7
13	74	66	5	0.6
14	78	70	7	0.3
15	77	61	12	1.2
16	87	59	27	0.8
17	76	64		
18	..	..	12	1.0
19	78	61	18	1.5
20	82	56	11	0.9
21	79	54	24	1.3
22	81	55	12	0.2
23	74	58	14	0.0
24	75	53	11	0.1
25	77	51	17	0.4

TABLE III *(continued)*.

Date	Maximum shade temperature	Minimum shade temperature	Atmometer loss (white sphere)	Atmometric index of solar radiation
	Deg., F.	*Deg., F.*	*Ml.*	*Ml.*
Nov. 26, '29	78	56	18	2.2
27	84	61	22	1.6
28	78	59		
29	83	54	73	5.7
30	83	44		
Dec. 1	80	47	..	...
2	75	52	12	0.0
3	82	63	19	0.6
4	81	50	18	0.5
5	82	54	20	2.7
6	84	58	22	2.4
7	81	57	17	0.7
8	82	64	20	2.1
9	80	57	18	1.2
10	80	59	16	1.2
11	74	60	14	0.3
12	77	49	12	0.0
13	87	60	14	0.3
14	92	72	17	1.0
15	89	69	19	1.2
16	84	70	15	0.2
17	89	65	14	0.0
18	84	72	10	0.4
19	84	76	12	0.6
20	87	59	23	1.0
21	87	55	22	1.5
22	83	59	14	0.0
Jan. 12, '30	..	..	20	0.0
13	..	..	14	0.2
14	86	..	11	0.0
15	86	71	14	0.4
16	82	62	16	0.5
17	83	54	19	1.0
18	78	57	17	0.0
19	88	56	22	2.0
20	81	50	18	0.6
21	83	61	16	0.2
22	86	54	15	0.0
23	94	51	20	1.0
24	81	51	25	3.0
25	85	50	45	2.8
26	80	56		
27	90	63	12	0.3
28	83	..	36	0.7
29	86	55		
30	81	56	14	0.1
31	88	50		
Feb. 1	86	56	86	4.6
2	85	62		
3	85	67		
4	84	..		
5	88	64		
6	81	60		
7	87	57		
8	89	56	196	7.8
9	80	59		
10	82	59		
11	83	54		
12	93	60		

TABLE III *(continued)*.

Date	Maximum shade temperature	Minimum shade temperature	Atmometer loss (white sphere)	Atmometric index of solar radiation
	Deg., F.	*Deg., F.*	*Ml.*	*Ml.*
Feb. 13, '30	88	59		
14	86	58	52	1.6
15	78	61		
16	84	44	23	0.9
17	87	47	19	0.7
18	94	58	27	0.6
19	95	63	31	1.5
20	101	71	36	1.2
21	94	70	35	1.0
22	87	65	24	1.0
23	80	65	14	0.6
24	88	62	23	1.6
25	91	72	33	2.2
26	79	64	13	0.4
27	88	56	22	1.4
28	93	56	28	1.4
Mar. 1	86	56		
2	75	56	54	2.5
3	78	50		
4	80	..	46	2.8
5	85	50		
6	..	..	26	1.0
7	..	..	56	4.5
8	..	..		
9	84	58	25	1.9
10	84	59	24	1.8
11	71	60	29	2.6
12	79	55		
13	83	56		
14	85	60	112	6.2
15	81	52		
16	88	53		
17	88	60		
18	87	71	89	7.0
19	81	64		
20	84	55	28	1.6
21	86	59	28	1.7
22	87	47	25	1.6
23	89	48	26	1.8
24	79	51	21	2.1
25	79	..	13	0.9
26	79	60	17	2.1
27	77	56	21	1.6
28	80	53	21	1.8
29	82	54	38	2.6
30	79	55		

sampling was generally adequate to give values fairly representative of the stands.

After the first weighing each rack with its seedling tops was transferred to an electrically controlled oven with maintained temperature of 105°, where it remained till loss of weight had ceased. The length of the drying period was regularly never less than 4 hours and never more than 12 hours. The racks

were then transferred to desiccators with dried calcium chloride, for cooling and transfer to the weighing room, where each seedling top was again weighed. The average dry weight per top was finally computed for each sample and the difference between the average green weight and the average dry weight was taken to represent the average moisture content of the seedlings in the bed in question at the time of sampling. All weighings were made to the fourth decimal place by means of an ordinary rider on the balance beam. The balance case was provided with a beaker of dried calcium chloride for the dry-weight weighings.

Early in the progress of the experiments it was found that the moisture content of the seedling tops fluctuated in a regular way with the alternation of day and night, being relatively high at night and relatively low in the daytime, as has been observed in a number of instances for other kinds of plants. This diurnal fluctuation rendered it necessary that the regular moisture-content samplings described above should be made in the very early morning, when the moisture content was nearly at its maximum and before the occurrence of the morning rise in transpiration rate. The work of sampling began between about 3:30 and 6 o'clock, early enough in every case so that all green-weight weighings for the day might be completed before sunrise. The number of these weighings to be made on any morning varied from 10 to 90.

Measurements of Soil-Moisture Conditions.—The initial water-supplying power of the soil in each seed bed was measured for a depth of 3 to 5 cm., at the time of the occurrence of a certain advanced stage of wilting in the plants, to be characterized below. Livingston soil points were employed. They were hollow porous-porcelain pieces, each with an upper section of cylindrical shape (2.5 cm. high and 2.2 cm. in diameter outside) continuous with a lower portion of conical form (5 cm. high), which terminated in a point. The whole piece was 7.5 cm. long and the wall was about 2 mm. thick. It was waterproofed outside except for an absorbing zone 2 cm. high, located on the conical part with its upper margin 3 cm. from the upper end of the piece. The area of the absorbing surface was about 12 sq. cm.

In this study the soil points were first weighed oven-dry, in tared glass test-tube-like containers with cork stoppers, one instrument in each container. They were then inserted vertically into the soil to their full length; which brought the absorbing zone into capillary contact with the soil between 3 and 5 cm. below the soil surface. After a 1-hour exposure they were lifted, quickly brushed to remove adhering soil grains and returned to their respective containers, in which they were again weighed. Weighings were to the nearest milligram. The amount of water absorbed during the 1-hour exposure in the soil (the difference between the two weights) was taken as a measure of the initial water-supplying power of the soil for the given depth. It represents the amount of water that an adequate absorbing surface

of 12 sq. cm. might take up in the initial hour of exposure to the soil mass in question, at a depth of 3 to 5 cm.

The soil points used in this study had been standardized by comparing their absorption when all were exposed for an hour, side by side and about 12 cm. apart, in a box of sand of nearly uniform moisture content. Three such calibrations were made, with sand of different water contents, absorption by a single point being about 72 ± 7 mg., 31 ± 5 mg. and 12 ± 1 mg., respectively. The deviation from the average is seen to be not far from $\pm$ 10 per cent. Deviations among a set of readings from several soil points exposed at the same time in the same box of soil are only partially due to differences in the instruments. They are likely to be higher or lower because of slightly different exposures to the surrounding soil (which is always somewhat compressed and otherwise disturbed when the instrument is inserted. Furthermore, different locations in the same soil mass are apt to differ considerably, as is generally shown when a presumably uniform soil mass is studied for water content by means of several samples taken at the same depth. The soil points themselves appear to be more nearly uniform in water-absorbing capacity (up to at least 2 gm. or more) than are the water-supplying powers of different soil locations at the same depth in the same supposedly uniform soil mass. It is of course to be remembered that plant roots must encounter just this same sort of deviation in the water-supplying power of the soil about them, as they are brought into contact with unexplored soil surfaces through elongation and the continuous formation of new absorbing surfaces.

With soils of very low water-supplying powers air-dried or even desiccator-dried soil points may fail to give satisfactory readings because their water-absorbing capacities may be too low at the beginning of an exposure. It sometimes occurs that an insufficiently dry soil point may lose water to the soil instead of taking up water from the soil, thus giving a negative reading, which may be disconcerting. When very dry soils are to be studied the instruments should be thoroughly dried and they should be inserted in the soil with little chance of their taking up significant amounts of water from the air just before insertion. For readings of 20 mg. or less some difficulties of this sort were encountered in the early stages of this study but such difficulties were finally avoided by drying all soil points at 90° for 16 hours or more. They were always allowed to cool in their closed containers before being weighed and applied to the soil.

The value of the soil-point method is dependent on the assurance that all water reaching the absorbing surface during the exposure period is absorbed very quickly. Only so long as the absorbing power of the instrument is greater than the supplying power of the adjacent soil can the amount of water absorbed in the standard exposure interval be taken as a measure of the dynamic soil feature in question. As water enters the instrument

the absorbing power of the latter decreases, of course, and this characteristic must eventually come to equal the supplying-power of the soil; after which the rate of absorption is determined by the condition of the instrument rather than by soil influences. It is therefore necessary that the exposure period should always be short enough so that the absorbing power of the porous-porcelain surface shall still exceed the supplying power of the soil at the end of the exposure. For wet soils (with high initial water-supplying powers) the exposure should be relatively short, while it may be very long if the initial supplying power of the soil being tested is very low. These considerations have received attention by Livingston and Koketsu, and Wilson. For the low supplying-power values dealt with in the present paper in the 1-hour exposure period was surely not too long. It might have been somewhat longer, but it is desirable that all comparable readings be obtained with the same exposure. The 1-hour period has been used by most workers who employed this method and appears to be very satisfactory.

The relation of soil-point values to corresponding water contents of the soil.—Soil-moisture conditions have generally been measured and defined in terms of the weight of water held in a given volume of soil or in a volume of soil containing a given weight of non-water material. Either of these methods is apparently useful in some ways, especially in studies dealing with the molecular attractions between the non-water particles of the soil and its contained water. When soil-moisture conditions are to be related to plant health, however, neither of these water-content criteria is satisfactory, for the influential condition that requires quantitative measurement is then not the *water-content* of any unit of soil, however defined, but the *capacity* of the soil to *supply water* (*i. e.*, soil solution) to the absorbing surfaces of the root system of the plant.

Because the same type of sand was used for all the beds during this study and all had very nearly the same packing, there should be a definite relation between soil-point readings and the corresponding water-content values of the soil computed either on the basis of weight or of volume. A special experiment was performed to bring out this relation for these beds. A bed was prepared just like those used for the seedlings but no seeds were planted in it. It was thoroughly watered and was then allowed to dry out until the soil had approximately attained the air-dry condition. Daily soil-point readings were made throughout this period for a depth of 1 to 3 cm. and for a 1-hr. exposure, three instruments being employed at each observation. Corresponding daily samples of soil from the bed, to a depth of 4 cm. were also taken, by means of a 1-cm. cork borer, which removed about 3.1 ml. of soil. For each soil-point reading this sample was taken a few centimeters away from the soil point. The dry weight and water content of each sample were ascertained in the usual manner

and each water-content value was finally computed as a percentage on the basis of the volume of the sample.

When the soil of this special bed had about ceased to lose water it was thoroughly wetted again and the experiment was repeated. For the first experiment drying out took 13 days, for the second it took 14 days. The corresponding total losses from the white atmometer sphere were 169 ml. and 167 ml. The results for the two series were very consistent. These results are shown in Table IV. Each soil-point reading and the corresponding volumetric water-content value were plotted as the rectangular coördinates of a point on coördinate paper and when all points for both experiments had been marked a smooth curve was drawn to represent the rate of decrease in soil-point readings with respect to the rate of decrease in volumetric percentages of soil water content. To obtain the gravimetric values of soil-moisture percentage it is necessary only to multiply each volumetric percentage by 0.70 throughout the series.

TABLE IV. *Water-content percentages corresponding to representative soil-point readings, for a depth of 2-3 cm. in a sand bed like those used for seedlings.*

Soil-point reading	Water-content (volumetric, on basis of soil volume)	Soil-point reading	Water-content (volumetric, on basis of soil volume)
Mg.	*Per cent.*	*Mg.*	*Per cent.*
0	0.2	150	5.8
10	0.6	200	7.0
20	1.0	250	8.0
30	1.4	300	8.8
40	1.8	400	9.7
50	2.3	500	10.2
60	2.7	600	10.6
80	3.5	700	10.8
100	4.2	800	11.0

For the kind of sand and the degree of packing employed in the beds the magnitude of the initial water-supplying power is approximately proportional to the volumetric water-content percentage, up to a supplying-power value of about 125 mg. or to a volumetric percentage of about 5. For the range from approximate air dryness to this limit the soil-point reading (in milligrams) corresponding to any volumetric percentage may be approximately ascertained by multiplying the corresponding percentage by 25; that is, the initial supplying power for the 2—3 cm. depth increases by about 25 mg. for each gram of water held in 100 ml. of the upper 4 cm. of soil. Beyond a supplying power of about 125 mg. this relation of proportionality does not continue and the supplying-power value increases at an accelerated rate. A graph showing these features may readily be constructed from the data given in Table IV. It must be remembered that these special relations refer specifically to the soil and packing of the sand beds and to the depths to

which the indices refer; and that other soils, other degrees of packing or other depths would be expected to show quite different relations between the dynamic index of soil-moisture condition and the corresponding static index. As long as the nature and packing of all soils in a series are alike, as in this study, either method for computing water content is equally good, since one series of percentages can be derived from the other by the employment of a simple coefficient; but of course the coefficient varies with the kind of soil and its state of packing, and water-content values cannot be compared when soil and packing are not alike throughout a series of observations. The dynamic index of soil-moisture condition cannot in general be deduced from water-content percentage, excepting by means of an empirically derived table of corresponding values such as those given in Table IV. However, for this particular study, and only for its background complex, this table may be used if one wishes to convert soil-point readings into the corresponding percentages. It is unfortunate that these water-content percentages refer to a depth of from 0 to 4 cm., while the corresponding soil-point readings refer to a depth of from 2 to 3 cm. and the soil-point readings for the seedling beds refer to a somewhat greater depth (3 to 5 cm.), but the errors of relationship introduced by these discrepancies are systematic and probably negligible considering the deviations encountered in this kind of experimentation.

RESULTS WITH NORWAY SPRUCE

Wilting and Drying of the Plants

The results secured with Norway spruce will be presented first, after which those for the other species will be set forth somewhat more briefly. At the time when watering was discontinued the leaves of the first whorl were just beginning to appear and the six or eight cotyledons represented practically all the foliage. Turgor throughout the plant was high. The cotyledons appeared glossy, the epidermis being tightly stretched, somewhat like the skin over a strongly flexed human knuckle. In a few days the appearance of the seedlings began to show effects of inadequate water supply. The epidermis gradually became less glossy and, as turgor decreased, reflected light less thoroughly. The color of the cotyledons also became duller. Between a highly turgid cotyledon and one with a low degree of turgidity the difference is similar (for some eyes, at least) to that between paper with a glossy and paper with a matt surface. Obvious wrinkling of the leaf epidermis soon set in and became more and more pronounced. Small longitudinal grooves were observed and the general dullness was further accentuated. After a time the small grooves appeared to run together to form larger grooves, which were produced unequally on different sides of the cotyledon and at different levels. The shrinkage thus indicated resulted in a flattening and twisting of the cotyledons. Twisting began near the cotyledon tip and proceeded toward the

base. A still later phase of drying showed the cotyledons severely twisted and flattened, pale green or fawny in color and exceedingly brittle. In this last phase they crumbled when rolled between the fingers. For Norway spruce the position of the cotyledons did not alter considerably during the drying-out process and, aside from the twisting of the cotyledons themselves, the seedlings as a whole had about the same general shape when air dry as when fully turgid. More advanced seedlings, with the true leaves of the first whorl large enough to be conspicuous, showed the beginning of twisting in those leaves somewhat before twisting was observed in the cotyledons.

While these changes were taking place in the cotyledons the hypocotyls passed through a similar series of progressive degrees of wilting and withering but they did not usually become markedly twisted. For most of the other species studied wrinkling and shrivelling were apparent in the cotyledons somewhat sooner than in the hypocotyl, but for Norway spruce wrinkling of the hypocotyl was generally observable slightly before the cotyledons wrinkled.

It appears that the onset of a wilting phase similar to what Briggs and Shantz ('11) called "permanent wilting" may perhaps be denoted for these Norway spruce seedlings by the appearance of obvious epidermal wrinkles and the beginning of twisting of cotyledons. In the following paragraphs this will be called the *critical phase of wilting*. Seedlings in the critical phase soon recovered if the bed was watered but those whose cotyledons had become brittle were irretrievable. Death apparently occurred in the last stage of wrinkling and twisting, just before brittleness began to develop.

Decreasing Water Content of Seedling Tops As Drying Went On

Data of moisture content of plant tops. Table V gives the data on seedling moisture content secured from nine beds of sand-grown Norway spruce, along with the corresponding records of water loss from the white atmometer sphere. Each water-content value appears in three forms. First is given the average of the actual water contents of all the tops in the "corrected" sample, as 29.9 mg. for May 27 in Experiment 1. Then follows the corresponding actual average of the water-content percentages of all tops in the corrected sample. Each individual water-content is expressed as a percentage of the corresponding dry weight and all these percentage values for the corrected sample are averaged to give the value shown, as 396 per cent. for May 27 in Experiment 1. Finally, this average percentage for each observation is expressed in terms of the average percentage for the first observation in the same experiment, the latter being considered as unity. Thus this relative percentage for the first observation is 1.00 in every experiment and the other relative values range from 1.03 (Feb. 18, Exp. 9) to 0.03 (Dec. 22, Exp. 2). To avoid possibility of confusion it may be emphasized that each value in the next to the last column of the table is the average of the individual water-

TABLE V. *Water-contents and dry weights of tops of sand-grown Norway spruce seedlings at times of successive observations in each experiment, together with corresponding cumulative values of water loss from the white atmometer sphere.*

Exp. no., etc.	Date of observation	Total corrected atmometer loss[1]	Average dry wt. per plant top.	Water content of plant tops		
				Average per top.	Ave. of water content percentages based on corresponding dry weights	
					Actual	Relative to 1st value as unity.
	(1929)	*Ml.*	*Mg.*	*Mg.*	*Per cent.*	
Exp. 1	May 27	0	7.6	29.9	396	*1.00*
24 da. period,	29	17	7.4	29.4	400	*1.01*
excessive	31	32	7.7	31.2	405	*1.02*
watering.	June 2	69	7.8	28.5	375	*0.95*
	3	85	7.8	25.0	332	**0.84**
	4	96	9.1	28.1	310	0.78
Exp. 2	Dec. 4	0	6.3	24.1	383	*1.00*
24-da. period,	6	38	6.2	24.7	385	*1.01*
standard	8	77	6.2	24.2	372	*0.97*
watering.	9	97	6.7	23.1	340	**0.89**
	10	115	6.6	22.0	323	0.84
	11	131	6.8	19.9	296	0.77
	12	145	5.7	17.0	300	0.78
	14	171	6.4	12.8	184	0.48
	18	232	6.4	5.9	92	0.24
	22	303	7.2	0.9	13	0.03
	(1930)					
Exp. 3.	Jan. 12	0	5.9	24.5	416	*1.00*
24- da. period,	14	34	5.7	23.8	414	*1.00*
standard	16	59	6.0	23.9	405	*0.97*
watering.	17	75	5.9	21.4	353	**0.85**
	18	94	5.7	18.7	324	0.78
	19	111	6.4	21.0	330	0.79
	20	133	6.3	19.0	301	0.72
	21	151	6.3	18.5	296	0.71
	22	167	6.6	17.9	283	0.68
	23	182	7.0	17.9	256	0.62
	24	202	6.6	13.7	206	0.50
	25	227	6.7	11.0	142	0.34
Exp. 4	Jan. 12	0	6.0	23.9	403	*1.00*
24- da. period,	14	34	5.8	23.4	401	*1.00*
excessive	16	59	5.9	23.0	387	*0.96*
watering.	18	94	6.3	21.8	346	**0.86**
	19	111	5.9	20.0	336	0.83
	21	151	6.6	20.0	302	0.75
	23	182	6.5	17.6	289	0.72
	25	227	6.5	10.8	206	0.51
Exp. 5.	Feb. 20	0	4.7	20.6	445	*1.00*
	22	71	5.2	21.1	374	0.84
24-da. period,	23	95	5.6	20.0	338	**0.76**
deficient	24	109	5.8	19.1	330	0.74
watering.	25	132	5.5	11.5	170	0.38
	26	165	5.7	8.9	113	0.25
	28	200	5.8	3.5	37	0.08

[1] From white sphere, since first observation.

TABLE V *(continued).*

Exp. no., etc.	Date of observation	Total corrected atmometer loss[1]	Average dry wt. per plant top.	Water content of plant tops		
				Average per top.	Ave. of water content percentages based on corresponding dry weights	
					Actual	Relative to 1st value as unity.
	(1930)	*Ml.*	*Mg.*	*Mg.*	*Per cent.*	
Exp. 6.	Mar. 20	0	5.7	23.1	411	*1.00*
	21	28	5.2	22.0	417	*1.02*
24-da. period,	22	56	5.3	21.7	405	*0.99*
standard	23	81	5.4	21.5	400	*0.97*
watering.	24	117	5.9	18.5	327	**0.80**
	25	128	6.0	17.9	300	0.74
	26	141	6.2	16.2	285	0.69
	28	179	5.6	10.0	172	0.42
	31	238	5.7	2.8	42	0.10
Exp. 7.	Feb. 13	0	7.8	17.0	219	*1.00*
	16	52	8.4	18.2	217	*0.99*
60-da. period,	17	75	7.9	17.0	216	*0.99*
standard	18	94	7.6	14.6	190	**0.87**
watering.	20	152	8.2	8.0	99	0.45
	22	223	8.6	2.4	26	0.12
	27	330	8.1	1.6	20	0.09
Exp. 8.	Jan. 15	0	7.9	17.0	216	*1.00*
	17	30	8.3	17.7	212	*0.98*
68-da. period,	18	49	8.6	17.5	203	*0.94*
standard	19	66	8.3	16.9	206	*0.95*
watering.	20	88	8.2	16.0	202	0.94
	21	106	7.9	15.7	199	0.92
	22	122	9.0	17.0	185	**0.86**
	23	137	8.9	13.3	149	0.69
Exp. 9.	Feb. 13	0	9.9	16.1	166	*1.00*
	16	52	9.2	15.2	167	*1.01*
97-da. period,	18	94	9.7	16.5	170	*1.03*
standard	20	152	9.0	15.0	168	*1.01*
watering.	22	223	9.4	12.1	127	**0.76**
	23	247	10.5	11.3	110	0.66
	25	284	10.0	11.4	116	0.70
	27	330	9.7	11.3	118	0.71
	Mar. 1	380	9.4	6.0	62	0.37
	4	434	10.1	1.3	13	0.08

content ratios of the several seedling tops in the given sample; it is not the quotient of the average water-content per seedling top (third from last column) divided by the corresponding average dry weight (fourth from last column). For example, for May 27 in Experiment 1 the average ratio of water-content to dry weight is 396, as given, while the ratio of the average water-content (29.9 mg.) to the average dry weight (7.6 mg.) would be 393. It was thought that the method of computation used would be somewhat more

precise than the less laborious one, but the discrepancies between the results obtained by the two methods are not significant in this particular study. The average green weights are not shown in the table but each green-weight value is of course simply the sum of the corresponding dry-weight and water-content values, both of which are given.

The atmometric totals.—In the third column of Table V are presented the corrected losses from the white atmometer sphere. For each observation date in each experiment the total atmometer loss is given for the period since the day after the last watering. This last watering corresponds, of course, to the last effective rain before the onset of a drought period under natural conditions. The nature of a drought period may be defined partly in terms of its duration and partly in terms of its evaporation conditions, which generally fluctuate in intensity from day to day. But, as Wilson ('27) has pointed out, atmometric losses integrate time and evaporational intensity and the total water loss from a suitable standard evaporation surface constitutes a useful measure of the evaporational character of the period considered, including the time factor. Cumulative atmometric water-loss, as given in Table V, may serve better than mere time for picturing the march of the environmental conditions that influence water loss from the plants and from the soil through evaporation. But the time data are also given in the table.

The dry weights.—Since water contents were computed as percentages of the corresponding dry weights, it is desirable to examine the dry-weight values in some detail. A study of the nine series of these for Norway spruce shows that the average dry weight of tops increased very slightly, if at all, during the experiment period. Throughout the period the seedlings apparently lost through respiration almost as much non-water material as was gained through photosynthesis. Absorption of non-water material from the soil was surely negligible in this connection. It is to be remembered that a relatively small amount of this material was discarded, since only stems and leaves were taken in the samplings, the roots being thrown away, and a very little of the material derived from the photosynthetic process went into the root portion of the plant. In this phase of development the roots were enlarging rapidly and their enlargement may have continued to some extent after enlargement of the aerial parts had ceased because of drought.

In Experiment 1 the average dry weight shows no significant alteration throughout the 9-day period, with the single exception of the last value. All values excepting the last lie between 7.4 and 7.8 mg. That the last value, for June 4, is as high as 9.1 mg. may be due to imperfect sampling of the stand of seedlings. This was the first experiment performed and some imperfections in technique of sampling were overcome in later experiments. Neglecting this exceptional value it may be said that the average dry weight of tops of these seedlings was about 7.7 mg. throughout the first experiment.

In Experiment 2 the last dry-weight value for the 19-day period is again the highest (7.2 mg.) but the next to the last is almost like the first (6.3, 6.4 mg.) and the lowest value (5.7 mg.) is for the 9th day. It appears that these plants had an average dry weight of about 6.4 mg. throughout the period and that the fluctuations shown are of negligible significance.

In Experiment 3 there seems, on the whole, to be some evidence of a slight increase in average dry weight during the 14 days of the experiment, as from 6.0 mg. to about 6.7 mg. The fluctuations are markedly inconsistent, however; we may note, for instance, that the lowest value (5.7 mg.) occurs for the third and again for the seventh day, while the highest value occurs for the twelfth day. The average dry weight for the whole period of this experiment is 6.3 mg.

In Experiment 4 the last three values are alike (6.6, 6.5 mg.) and high, but the value for the eighth day of the 14-day period is low and like that for the fifth day (5.9 mg.), while the value for the first day is about the same (6.0 mg.). The average for the period is 6.2 mg.

In Experiment 5 there is again some evidence of an increase in dry weight during the 9 day period, but the highest value (5.8 mg.) occurs for the fifth day as well as for the ninth. The average for the period is 5.5 mg.

In Experiment 6 there seems to be no evidence of increase in dry weight and the average of all values for the 12 days is 5.7 mg., which happens to be the actual value shown for the first day and the last.

The results for Experiment 7 are similar to those of Experiment 6 in this regard, with an average dry weight of 8.1 mg. for the 15-day period. These plants had been watered for about 60 days (instead of 24) after they emerged from the soil and before the beginning of the drought period.

The plants of Experiment 8 had been watered for 68 days after emerging from the soil. The record of average dry weights shows some evidence of increase, from about 8.3 mg. (second day of the 9-day experiment period) to about 8.9 mg. (last day), but the lowest value (7.9 mg.) occurs for the seventh day as well as for the first. The average for this experiment is 8.4 mg.

For Experiment 9, with seedlings that had been watered about 97 days before the experiment began, there is no evidence of any significant increase in dry weight during the 20-day period. The first and last values are essentially alike (9.9 and 10.1 mg.) and the highest value (10.5 mg.) occurs for the eleventh day. The average for this period is 9.7 mg.

To summarize—Dry weights surely did not decrease during the experiment periods and if they increased the increment was very small, so small as to be negligible in considering the use of dry weight as the basis for computing the comparative indices of plant water content. The average dry weights per seedling for the nine experiments with Norway spruce are 7.7, 6.4, 6.3, 6.2, 5.5, 5.7, 8.1, 8.4 and 9.7 mg. The three highest averages (Ex-

periments 7-9) are for seedlings that were much more advanced in development than those of the other experiments. The non-water material probably began to increase in these Norway spruce seedlings when they had been about four or five weeks above the soil. This increase should be very slow at the start but its summation apparently became considerable in a period of two or three months. The seedlings of Experiment 1 showed a much higher dry weight of tops than did any of the other lots of 24-day seedlings. This may be related to the fact that Experiment 1 was performed in May and June, with long daylight periods and high light intensities, while all the other seedlings were grown between November and March. Omitting Experiment 1, it may be said that seedlings about 24 days old (counting from their appearance above the soil) had dry weights of about 6.0 mg., while those about 60 days old had dry weights of about 8.3 mg., and the dry weights of those about 97 days old were about 9.7 mg. The rate of increase in non-water material should of course have been increasingly accelerated as the seedlings developed, especially after the first whorl of true leaves began to appear.

The diurnal fluctuation in water content of tops of healthy seedlings.—It has been mentioned that all seedling samples were taken in the early morning, shortly before sunrise, so as to have them represent the seedling population of their respective beds at about the time of the maximal water content for the day. In this connection it will be interesting to present the results of a special series of measurements of plant moisture, made in the usual way by means of 10-plant samples from a bed of 26-day-old Norway spruce seedlings rooted in well watered sand, the samples being taken at 2-hour intervals for a 24-hour period. This special experiment was begun on the morning of March 21, 1929. The day was cloudless, without unusual meteorological influences. The average water contents per seedling are shown in Table VI.

TABLE VI. *Average water-contents of Norway spruce seedlings.*

Time of observation	Average water content per plant	
	As percentage of dry weight	Relative to highest value
Hour of day (Mar. 21)	*Per cent.*	
6	417	1.00
8	415	1.00
10	393	0.94
12	394	0.94
14	385	0.92
16	380	0.91
18	397	0.95
20	401	0.96
22	405	0.97
24	397	0.95
(Mar. 22)		
2	411	0.99
4	408	0.98
6	405	0.97

The average moisture content of these seedling tops decreased as much as 9 per cent between the sixth and the sixteenth hour, but nearly complete recuperation occurred in the next few hours. Only one experiment of this kind was carried out but the results agree with what should be expected from our knowledge of the diurnal fluctuation of water content in leaves and stems generally. This sort of fluctuation was suggested by Renner ('11) and definitely pointed out by Livingston and Brown ('12). It has been reported in several more recent papers (Lloyd, '12; Edith B. Shreve, '14; Krasnoselsky-Maximov, '17; Bachmann, '22; Knight, '22; Mina and Butovski, '23; Maximov and Krasnoselsky-Maximov, '24). It is of course due to the fact that daytime transpiration is more rapid than water absorption and conduction to the transpiring parts, whereas absorption and conduction are more rapid than transpiration in the earlier hours of the night. Thus the saturation deficit incurred during the day is made up at night.

Early-morning water contents of healthy Norway spruce seedlings, before drought effects were apparent.—In each experiment the average water content per seedling top for the first observation after watering was discontinued may be taken to represent the seedlings before any injury due to moisture deficiency began. In the series of relative water-content values for each experiment (last column of Table V) the value for the first observation is always taken as 1.00, as has been said, but it will be noticed that the highest water-content value for an experiment is not always recorded for the first observation. When a later observation gives a relative value greater than that for the first the highest value may be 1.01, 1.02 or 1.03 and it may occur for an observation as late as the third, as in Experiments 1 and 9. This fluctuation is very slight, however, and it is not to be regarded as significant under the circumstances of this study. These three higher values are consequently considered as practically equivalent to 1.00.

Of course there is no way of detecting the very first stage of injurious moisture deficiency by inspection, but it may be supposed that the seedlings were still in good health until the relative water-content value had decreased somewhat below 1.00. In accordance with the general appearance of the seedlings one may tentatively, and somewhat arbitrarily, set the lower limit of relative water-content for health at between 0.94 and 0.95. It is reasonably sure that values above 0.94 always represent seedlings in which considerable turgor was still present throughout the leaves and stems, even though incipient drying of some tissues may have begun. From these considerations, a seedling may be regarded as still in a healthy condition as long as the relative water-content of its top is between 0.95 and 1.03, inclusive. All relative values above 0.94 are printed in italics in the last column of Table V.

It is interesting to note that the relative water-content values remained above 0.94 from 1 to 8 days after watering had been discontinued. Through-

out this period it is probable that the soil was gradually drying out but that its water-supplying power was still adequate to maintain health. The drying process was apparently more rapid for some experiments than for others, however, and the conditions that influenced the rate of drying of both soil and plants are presumably represented by the respective concomitant atmometer losses. A shorter period with more intense evaporation should lower the water-supplying power of the soil and the water-content of the seedlings as much as a longer period with sufficiently less intense evaporation. Also, if the soil were drier at the beginning of one experiment than at the beginning of another, a shorter period without watering should be required in the first instance to bring about the beginning of drought effects on the plants. Finally, if the root systems of the plants extended more deeply into the soil or were otherwise more extensive or more active at the beginning of one experiment than at the beginning of another, or if the water-absorbing or water-retaining power of the plants of one experiment were greater than in the case of another experiment, then the first effects of drought would be more tardy in their appearance in the former instance. With these suggestions in mind one may examine the available data on the retention of a healthy condition after watering had ceased. The values to be examined are assembled in Table VII, and are derived from Table V.

TABLE VII. *Data for Norway spruce seedlings, on the maintenance of relative average water contents of tops above 0.94, for the period of apparent health after watering had ceased.*

Exp. No., seedling age, treatment	Length of period in days	Atmometer loss for period in Milligrams	Ave. initial water content of tops expressed as percentage of dry weight,%	Initial ave. water content of tops, *Mg.*	Initial ave. dry weight of tops, *Mg.*
No. 1, 24 da., e.w.*	7	69	396	29.9	7.6
No. 2, 24 da.....	5	77	383	24.1	6.3
No. 3, 24 da.....	5	59	416	24.5	5.9
No. 4, 24 da., e.w.*	5	59	403	23.9	6.0
No. 5, 24 da., d.w.*	1	36 (?)	445	20.6	4.7
No. 6., 24 da.....	4	81	411	23.1	5.7
No. 7, 60 da.....	5	75	219	17.0	7.8
No. 8, 68 da.....	5	66	216	17.0	7.9
No. 9, 97 da.....	8	152	166	16.1	9.9

* The abbreviation *e.w.* denotes excessive watering; *d.w.*, deficient watering. All experiments not designated by one of these abbreviations had standard watering.

For experiments 2, 3, 4, 7 and 8 high water-content of tops was maintained for 5 days after the beginning of the drought and for Experiment 6 this period of high water-content was 4 days. For Experiment 1, however, the period of high water-content was 7 days. In all of these seven instances the corresponding atmometer losses were nearly alike. Their average is 69 ml., the actual loss recorded for the 7 days of Experiment 1. The lowest of these atmometer losses is 59 ml. (Exps. 3 and 4) and the highest is 81 ml. (Exp. 6). It may therefore be said that these seven experiments agree within about plus or minus 15 per cent of their average. Without attempting any great degree of precision (which would not be warranted in such a study as this) it appears that about 69 ml. of water (say between 60 and 80 ml.) was lost from the standard white atmometer sphere between the cessation of water and the end of the period of high (healthful) water contents as here defined.

This mean atmometer loss represents an integration of both time and the intensity of the atmometric conditions and it is more satisfactory for our present purpose than are the time indices alone. The time indices for these seven experiments are 7, 5, 5, 5, 4, 5, and 5 days, as has been noted, and their average is 5.14 days. The shortest period (4 da.) is 22 per cent less than the average and the longest is 36 per cent greater than the average. A healthy condition seems to have been maintained for from 4 to 7 days after watering was discontinued.

In the single instance where watering had been only barely adequate to maintain growth (Exp. 5), the drought influence was shown after only a single day and the corresponding atmometer loss is estimated as 36 ml., half of the loss for the day. This constitutes an exceptional case, the explanation of which seems to lie in the fact that this bed had an unusually low initial moisture content. Also, the seedlings themselves may have been different from those of the other 24-day beds, because of deficient water supply throughout their growing period.

The other obviously exceptional case is that of Experiment 9, in which the tops maintained an average relative water-content above 0.94 for 8 days after watering had been discontinued, during which period the standard white atmometer sphere lost 152 ml. of water. This exceptionally high value may have been due to more extensive or more efficient root systems, or to some other plant characteristic for the seedlings of Experiment 9 were 97 days old when watering was discontinued. It is notable, however, that the seedlings of Experiments 7 and 8, which were 60 or 68 days old at the beginning of the period without watering, do not appear to have been exceptional in this way; they behaved very much like the 24-day seedlings of Experiments 1, 2, 3, 4, and 6, which had received standard or excessive watering.

The absolute water-content percentages on the day after watering was discontinued ranged between 383 and 416 for the 24-day seedlings with either

standard or excessive watering. This constitutes a fairly close agreement among these beds and indicates that healthy seedlings of this class were characterized by a water-content of tops of 399 ± 16 per cent, on the dry-weight basis. For Experiment 5, the single experiment with deficient watering, the causal relations of the unusually high percentage of 445 are difficult to surmise, though several possibilities might be suggested.

A very striking point brought out by Table VII is that the older seedlings (with standard watering) were characterized by exceptionally low water-content percentages when still in good health. While the 24-day seedlings gave an average water-content of tops of about 399 per cent, the 60-day and 68-day stands (Exps. 7 and 8) gave average water-contents of tops of only 219 and 216 per cent and the corresponding percentage for the 97-day stand (Exp. 9) was as low as 166. These observations are worthy of study, for the water-content percentage is of course a ratio (water-content divided by dry weight) and when the value of a ratio changes the change may be due to a change in the numerator, to a change in the denominator or to both acting together. To examine this interesting state of affairs it is essential to consider the average actual water-content and the average actual dry weight for the beginning of each experiment. These values are shown in the last two columns of Table VII. They correspond, in each case, to the initial water-content percentage, which is taken as unity for the relative percentages of Table V.

Omitting Experiment 5 (with deficient watering), we may average the initial actual average water contents for all cases of 24-day seedlings with either standard or excessive watering, for their deviations are not great. The result is 25.1 mg. The corresponding initial average dry weight for this 24-day class with standard or excessive watering is 6.3 mg. For the healthy 60- to 68-day seedlings with standard watering, the average water content is 17.0 mg. and the average dry weight is 7.85 mg. And for the 97-day seedlings these averages are 16.1 mg. and 9.9 mg. respectively. In the 40 days of culture between the 24-day stage of development and the 60- 68-day stage the average amount of *non-water material* per seedling top increased from about 6.3 mg. to about 7.9 mg. (or from 1.00 to 1.24) and in the 73 days ending in the 97-day stage it increased from about 6.3 to about 9.9 mg. (or from 1.00 to 1.57). For the same periods the *average water-content per top* decreased from 1.00 to about 0.68 (60—68-day class) and from 1.00 to about 0.64 (97-day class). For the 60-to-68-day seedling the water-content percentage decreased from 1.00 to about 0.55 and for the 97-day seedlings this change was from 1.00 to about 0.42. In the first instance the dry-weight increase was about 18 per cent more effective in lowering the percentage value than was the water-content decrease. In the second instance the dry-weight increase and the water-content decrease were about equally effective.

Changes in average dry weight and average water content as the seedlings developed during the period of watering.—What was said in the last portion of the preceding subsection led to the interesting conclusion that, beginning with healthy seedlings 24 days old (from the time they emerged from the soil), the average dry weight per seedling top increased and the average water content per top decreased, while watering was still being continued. More detailed data bearing on this point were secured by sampling the stands for Experiment 7, 8 and 9 at intervals in the latter part of the period of watering, before the experiments on drought effects were begun. The first sampling occurred when the seedlings were 28 days old. The numerical results are shown in Table VIII, which includes some of the values shown in Table V.

Because the data in Table VIII are of special interest with reference to the internal water relations of such seedlings as these while still in a

TABLE VIII. *March of average dry weight and average water-content of healthy Norway spruce seedlings, beginning after the plantlets emerged from the soil.*

Exp. No.	Date of observation (1930)	Age of seedlings, *Days*	Average dry weight per seedling top, *Mg.*	Average water-content per seedling top	
				Absolute, *Mg.*	On basis of dry weight, *Per cent.*
7	Jan. 12	28	5.4	21.9	407
	Jan. 14	30	5.7	22.0	389
	Jan. 19	35	5.8	20.2	348
	Jan. 28	44	6.7	18.0	269
	Feb. 13*	60	7.8	17.0	219
	Feb. 16*	63	8.4	18.2	217
	Feb. 17*	64	7.9	17.0	216
8	Dec. 6	28	5.9	24.9	419
	Dec. 10	32	6.1	22.5	372
	Dec. 19	41	6.5	21.6	334
	Dec. 25	47	7.0	20.9	302
	Jan. 11	64	8.1	17.7	221
	Jan. 13	66	7.4	17.1	232
	Jan. 15*	68	7.9	17.0	216
	Jan. 17*	70	8.3	17.7	212
	Jan. 18*	71	8.6	17.5	203
	Jan. 19*	72	8.3	16.9	206
9	Dec. 6	28	6.4	25.9	396
	Dec. 10	32	6.4	23.8	376
	Dec. 19	41	6.1	21.3	352
	Dec. 25	47	6.3	20.2	323
	Jan. 11	64	8.5	18.3	219
	Jan. 17	70	8.6	19.2	225
	Jan. 28	81	8.6	18.1	198
	Feb. 13*	97	9.9	16.1	166
	Feb. 16*	100	9.2	15.2	167
	Feb. 18*	102	9.7	16.5	170
	Feb. 20*	104	9.0	15.0	168

* Data for the dates marked with asterisks are repeated from Table V.

healthy condition, as in a nursery bed, they are shown graphically in Fig. 1. The graphs for average water-content and average dry weight per seedling top (both of which are expressed in milligrams) are all plotted on the same ordinate scale but the graphs for water-content percentage are on another scale of ordinates and each one has been shifted arbitrarily so as to make its first point coincide with the first point on the corresponding graph of average water-content. All graphs are plotted on the same scale of abscassas, which shows the dates of observation and the increasing ages of the seedling stands. These data show how the average dry weight per seedling top increased, from 28 days after appearance above the soil to the end of the series of observations, and how the average actual water-content per seedling top decreased. If these values were to continue to alter in the manner shown there should come a time when the non-water material would equal and surpass the corresponding water-content. It is also clearly shown how the water-content percentage, on the dry-weight basis, decreases with the progress of development, at a rate much more rapid than that at which the actual water-content decreases. These observations substantiate the conclusions brought forth inductively in the latter part of the preceding subsection.

The graphs of water-content of tops.—The relative values of the water-content percentage on the basis of dry weight (the last column of Table V) are shown for the nine experiments with Norway spruce by the continuous-line graphs of Figures 2 to 10, where total atmometric losses since the beginning of the drought period are plotted on the axis of abscissas and the relative values of plant water content are ordinates. The observation dates corresponding to the several atmometric values are shown on the upper margin of each figure, so that simple time relations may be read directly. Each graph shows by its slope the varying rate at which the average water content of the stems and leaves altered with respect to the progress of water loss from the standard evaporating surface of the white atmometer sphere during the period of the experiment.

Every one of these graphs starts with an ordinate of 1.00 but soon bends downward. A circle on each graph marks the points for an ordinate of 0.95, which, as has been said, may be taken to represent in each experiment about the end of the period of health. The downward slope is maintained, in general, to the end of the graph, some experiments having been continued long enough to bring the last ordinate to a value below 0.10. On each graph the ordinate value corresponding to the attainment by the plants of the critical stage of wilting is indicated by a short horizontal line across the graph. As has been said, this stage (of notable shrivelling of stem and leaves accompanied by the beginning of apparent twisting) may correspond rather closely to the onset of the phase called "permanent wilting" by Briggs and Shantz

('11) and later writers. The soil-moisture graphs, which are the broken lines in these figures, will receive attention farther on, after these plant graphs have been examined.

Water-content of tops at the critical stage of wilting.—It is important to enquire whether the attainment of the critical stage of wilting in these Norway spruce seedlings might have been detected by means of water-content measurements, which might thus have replaced the less precise and somewhat impressionistic ocular observations on wrinkling and twisting. The water-content percentages that correspond to the critical degree of wilting are shown in bold-face type in the last column of Table V and they are also indicated on Figures 2 to 10, as has just been noted. Table IX shows the absolute and relative values of this percentage for each of the nine experiments with Norway spruce seedlings. It is at once clear that the *absolute*

TABLE IX

Exp. n., seedling age, and treatment	Water-content percentage of tops, on basis of dry weight at critical stage of wilting.	
	Absolute	Relative
	Per cent.	
Exp. 1. 24 da., excessive watering....	332	0.84
Exp. 2. 24 da., standard watering....	340	0.89
Exp. 3. 24 da., standard watering....	353	0.85
Exp. 4. 24 da., excessive watering....	346	0.86
Exp. 5. 24 da., deficient watering....	338	0.76
Exp. 6. 24 da., standard watering....	327	0.80
Exp. 7. 60 da., standard watering....	190	0.87
Exp. 8. 68 da., standard watering....	185	0.86
Exp. 9. 97 da., standard watering....	127	0.76

water-content percentage is not a constant throughout the series. Somewhat like the corresponding value for healthy seedlings at the beginning of the period without watering, it appears to approach constancy for the first six experiments (24-day seedlings) and for experiments 7 and 8, but its magnitude is very different for the three age classes. For the 24-day seedlings (Experiments 1 to 6) the average water-content percentage at critical wilting is 339 with a range from 327 to 353. For the 60-68-day seedlings (Experiments 7, 8) the two available values are 190 and 185, with an average of 188. For the 97-day seedlings (Experiment 9) the only available value is 127. Although the data for the more advanced seedlings are not so numerous as is desirable, it is clearly indicated that the absolute water-content percentage at the critical stage varied with the initial state of the plants, being smaller as the plants were more advanced in development. This conclusion would be expected from what has been said concerning the corresponding absolute

values for the time when watering was discontinued, while the plants were still unaffected by water deficiency.

Turning to the *relative* values of these water-content percentages at the critical stage of wilting, the range of these for the entire series of 9 experiments is only from 0.76 (Experiments 5 and 9) to 0.89 (Experiment 2) and the distribution of the variations at once suggests that one is here dealing with an approximately constant index. The range is remarkably narrow, considering the difficulty of fixing upon the critical degree of wilting by ocular observation. For instance, there was considerable doubt in Experiment 5 whether the critical stage was really attained on February 22 or on February 23. If the earlier date had been recorded, then the critical relative-percentage value would have been 0.84 instead of 0.76. Similarly the critical value 0.76 in Experiment 9 may be somewhat too low and the value 0.89 in experiment 2 may be somewhat too high. In this connection it is to be remembered that the progress of wilting and the decrease in water-content of tops was recorded only at day intervals because the diurnal fluctuation of turgidity and seedling water-content precluded the employment of more frequent observations. No great precision could be expected from daily observations on these rapidly and continuously changing features, even if the ocular criteria for the attainment of critical wilting had been wholly satisfactory, which they were not. However, taking the figures as they came, the average relative water-content percentage for the critical wilting stage of these Norway spruce seedlings is indicated as about 0.83 ± 7. It is important to note that this critical value appears to have been approximately constant for all ages of seedlings employed and for all degrees of watering.

These results suggest that relative water-content percentage of tops might have served as a criterion for detecting a critical stage of wilting corresponding to the onset of what has been termed permanent wilting and that it might have been more satisfactory than ocular observation. For these experiments with Norway spruce seedlings we might say that this critical stage was attained when the water-content of tops, on the basis of dry weight, had been decreased by about 15 or 20 per cent of the corresponding value for the healthy plants before drought influence set in. Considering the extremely complex nature of wilting relations, this statement must be regarded as of a fair degree of precision. At any rate it is more satisfactory than any possible statement about the advent of the beginning of permanent wilting that might be based on ocular observation of wrinkling and twisting alone.

A second critical value of the water-content of tops.—Another critical moisture content of seedling tops appears on some of the graphs for Norway spruce (Figs. 2-10) and is suggested on others, in the region of ordinate values about 0.70 or 0.80. When this critical value appears it is immediately followed by a temporary retardation in the rate of decrease in water-content, which is followed in turn by the final rapid decrease that leads to desiccation.

Experiment 1 (Fig. 2) was not continued long enough to show this feature. The graph for Experiment 2 (Fig. 3) shows a retardation in the rate of water loss between ordinates 0.77 and 0.78, for December 11 and 12. The graph for Experiment 3 (Fig. 4) is similar, with a retardation between ordinates 0.78 and 0.79, for January 18 and 19. On the graph for Experiment 4 (Fig. 5) there is a suggestion of a region of slower decrease in water-content between ordinates 0.75 and 0.73, but this may not be significant. The graph for Experiment 5 (Fig. 6) shows a region of retardation immediately beyond the main critical point, between ordinates 0.76 and 0.74, for February 23 and 24. As has been suggested, the main critical value may be somewhat too low in this case. In a similar manner, the graph for Experiment 6 (Fig. 7) suggests a region of retardation in water-content decrease between ordinates 0.80 and 0.74, for March 24 and 25, immediately beyond the point for the main critical stage of wilting. The graph for Experiment 7 (Fig. 8) shows no retardation at all. The one for Experiment 8 (Fig. 9) shows no region of retardation corresponding to the others, although it shows a definite one between the two ordinates of 0.94, preceding the permanent-wilting point. This appears not to be significant. A 4-day retardation is shown on the graph for Experiment 9 (Fig. 10), between ordinates 0.66 and 0.71, for February 23 and 27.

It does not seem likely that the water-content percentage is to be taken as actually *increasing* in this region of retardation in its rate of decrease, as appears on the graphs for Experiments 2, 3 and 9 (Figs. 3, 4, 10). For the present it seems best to conclude simply that the onset of the critical stage of wilting appears generally to have been followed by a temporary slowing of the rate of water-content decrease, perhaps resulting from the breaking of the tensile water columns in the vessels. This may correspond to the temporary rise in transpiring power reported by Bakke ('15) and Nichiporovich ('26). Bakke suggests that the rise may be due to the rupture of the tensile water columns.

As far as the writer is warranted in generalizing at present, he may say that the data of Tables V and VII and the graphs of Figures 1-9 indicate the following picture of the drying out of these seedlings. For about five days after the water has been cut off the water-content of the tops shows little diminution. But after about this interval the water-content decreases rather rapidly to the onset of permanent wilting (when about 17 per cent of the original water-content has been lost). Wilting continues and when about 25 per cent of the original water-content has been lost a temporary slowing of the rate of decrease in water-content is apt to occur; after this drying proceeds rapidly to the point of desiccation. Death may perhaps occur when about 30 or 40 per cent of the original water-content is lost, but this is uncertain for the lethal point has not been carefully studied.

The Initial Water-Supplying Power of the Soil, as Related to Wilting and to the Critical Water-Content of Tops

When the critical stage of wilting had been reached, or was seen to be approaching, frequent soil-point readings on the sand bed were begun and continued for several days or longer. These were made when the seedling samples were taken, shortly before sunrise. From three to five simultaneous readings, with different soil points and different locations, were regularly made at each observation and the results were averaged. It will be remembered that the soil-point reading represents the number of milligrams of water absorbed from the soil by a single soil point in one hour and that these readings are for a soil depth of from 3 to 5 cm. They serve as indices of the initial water-supplying power of the soil at the depth in question, referring to an absorbing area of about 12 sq. cm. For example, a reading of 24 mg. is taken to indicate that the soil adjacent to the instrument was capable of supplying water to the absorbing surface at a rate such that 24 mg. was supplied in the first hour after the placing of the soil point. Since the absorbing area of the instrument is about 12 sq. cm., this means that the soil adjacent to the absorber (which had been slightly compressed through the insertion of the latter) was capable of supplying 2 mg. of water per square centimeter of absorbing surface in the first hour after capillary contact had been established. The data from these readings are shown in Table X. They are given in full because they are of interest in connection with the usefulness of the soil-point method as well as in connection with the special problem of this study. For each experiment the average value that corresponds to the critical water-content and critical wilting stage of tops is shown in boldface type.

For Experiment 1 only one series of soil-point readings was made, corresponding to what the writer is considering as the onset of permanent wilting in the seedlings. For each of the other experiments two or more series of soil-point readings were made and in most cases the critical value (last column of Table 10) is for the second or third observation. The data in the last column of Table X are shown graphically by points and broken lines in Figs. 2—10, along with the corresponding graphs of water-content of seedling tops, and the critical point is marked by a value in parentheses. The ordinate scale for the water-supplying power values is numerically the same as for the relative water-content values, but the unit for the former is 1 mg. instead of 0.01. Thus, in Fig. 2, the point for a supplying power of 59 mg. is located on the level of 0.59 as read on the scale at the left.

The data and graphs for Experiments 3, 4 and 5 (Figs. 4—6) furnish a picture of the sort of results secured by means of soil points. The soil index is seen to have increased more rapidly than the water-content of seedling tops for the period under observation. Of course this decrease in the initial water-supplying power of the soil is due to the gradual drying of the soil,

TABLE X. *Soil-point readings, showing initial water-supplying powers of the soil at the 3-5 cm. depth in beds of Norway spruce.*

Exp. No., etc.	Date of Observation	Water absorbed by single soil point in 1 hr.					
		Individual tests					Average
		a	b	c	d	e	
	(1929)	*Mg.*	*Mg.*	*Mg.*	*Mg.*	*Mg.*	*Mg.*
Exp. 1.							
24 da., excessive watering	June 3	49	54	58	62	71	**59**
Exp. 2.	Dec. 8	31	34	34	38	42	36
24 da., standard watering....	9	24	25	27	27	29	**26**
	10	19	19	22	24	24	22
	11	12	15	22	24	24	19
	22	4	7	10	111	—	11
	(1930)						
Exp. 3.	Jan. 14	91	95	100	—	—	95
	16	37	39	40	—	—	39
24 da., standard watering....	17	24	26	28	28	—	**27**
	18	18	23	24	29	—	**24**
	19	15	17	20	20	—	18
	20	17	19	21	25	—	20
	21	13	14	15	—	—	14
	22	11	12	14	16	—	13
	23	10	10	10	12	—	10
	24	6	7	9	12	—	8
	25	4	4	6	8	—	6
Exp. 4.	Jan. 16	110	129	144	—	—	128
	18	49	59	60	62	—	**58**
24 da., excessive watering....	19	29	32	35	—	—	32
	21	17	18	18	—	—	18
	23	20	21	21	22	—	21
Exp. 5.	Feb. 20	102	129	162	—	—	131
	22	24	27	30	31	—	28
24 da., deficient watering....	23	20	20	21	21	—	**20**
	24	14	15	15	15	—	15
	25	12	12	13	16	—	13
	26	10	10	12	15	—	12
Exp. 6.	Mar. 20	87	97	107	113	—	101
24 da., standard watering....	24	22	25	27	29	—	**26**
Exp. 7.	Feb. 17	25	28	29	33	—	29
	18	18	18	18	26	—	**20**
60 da., standard watering....	20	10	10	11	16	—	12
	22	9	10	11	—	—	10
Exp. 8.	Jan. 17	26	30	41	—	—	32
	18	24	27	34	—	—	28
68 da., standard watering....	19	16	17	17	18	—	17
	20	13	14	14	16	—	14
	21	10	14	14	17	—	14
	22	9	12	13	15	—	**12**
Exp. 9.	Feb. 16	29	31	—	—	—	30
	18	19	19	25	—	—	21
97 da., standard watering....	20	17	20	22	—	—	20
	22	16	17	17	19	—	**17**
	23	11	11	12	13	—	12

under the influence of direct evaporation and of water absorption by the seedling roots.

One of the main purposes of the present study was to gain information concerning the relations between the decrease in the value of the initial water-supplying power of the soil and the onset of a critical stage of wilting, as a drought period continued. With this in mind one may now examine the soil-point values corresponding to the critical degree of wilting. These are the values shown in boldface type in the last column of Table X and specially marked in parentheses in Figs. 2—10. They are assembled below, arranged according to the conditions of the experiments from which they were derived.

For 24-day seedlings with standard watering: 26 mg. (Exp. 2), 27 mg. (Exp. 3), 26 mg. (Exp. 6).

For 24-day seedlings with deficient watering: 20 mg. (Exp. 5).

For 24-day seedlings with excessive watering: 59 mg. (Exp. 1), 58 mg. (Exp. 4).

For 60- to 68-day seedlings with standard watering: 20 mg. (Exp. 7), 12 mg. (Exp. 8).

For 97-day seedlings with standard watering: .17 mg. (Exp. 9).

It appears that the initial water-supplying power of these Norway spruce beds at the 3—5 cm. depth, at the critical stage of wilting in the plants, was not the same for all experiments in this series. It differed according to the previous treatment of the seedlings and according to their age or stage of development. This might be expected from the general consideration that plant and soil and air constitute a single dynamic system, the environment and the plant operating together, as has been emphasized by Livingston ('29). The 24-day seedlings with standard watering had roots whose absorbing surfaces were mostly within the soil-depth range referred to by the soil-point readings and the three cultures of this group were probably very nearly alike in all essentials. For these the critical water-supplying power may be taken as 26 mg. It has been mentioned that the critical wilting stage in Experiment 5 may have occurred on February 22 instead of February 23, and if that were true the critical soil value for that experiment would be 28 mg. instead of 20 mg., which would bring the seedlings with deficient watering into the same class with those that received standard treatment. The writer's information on the relations of deficient watering does not warrant further special consideration of this single case. The 24-day seedlings with excessive watering (Exps. 1 and 4) do require special consideration, however, for these are two cases which agree in having the same very high index of water-supplying power (58, 59 mg.) at the advent of critical wilting. The excessive-watering treatment had retarded root development in these two beds (Table II) and may also have lowered the capacity of the roots to absorb water. The absorb-

ing surfaces of the roots of these excessively watered seedlings were nearer the soil surface than was true for the 24-day seedlings with standard watering. Whatever may be the reasons, the excessively watered seedlings passed into the critical wilting stage when the sand of their beds at the depth tested still showed an initial water-supplying capacity more than twice as great as that shown by the same kind of soil at the same depth when seedlings that had received standard treatment attained the critical wilting stage.

For the older seedlings (Exps. 7, 8 and 9) the critical soil-point index is seen to be remarkably low (12, 17, 20 mg.). These seedlings held their water more tenaciously than did the 24-day seedlings and they wilted more gradually. It may well be that their longer root systems were drawing much of their water supply from soil depths greater than that of the soil-point readings. These roots were observed to be more branched and longer than those of the younger seedlings, a fact which supports this suggestion. Several other possible explanations might be mentioned, perhaps involving differences in the water-conducting systems of the plants of the two age classes. No differentiation based on these soil-point readings can be made between the two classes of older seedlings, however.

RESULTS WITH NORWAY PINE

General Appearance During Wilting

Experiments 10—14 were with Norway pine. The results of these will now be presented and discussed, principally from the standpoint of how they differed from or in what respects they were similar to the corresponding Norway spruce values.

The general appearance of the Norway pine seedlings as they became seriously wilted and withered did not differ greatly from that of the Norway spruce seedlings in a corresponding state. The first sign of wilting in Norway pine was that the cotyledons became duller in color. This was followed by wrinkling, barely discernible at first but gradually becoming so severe that the tips of the cotyledons were very much twisted. As desiccation progressed the seedlings ultimately became brittle and would crumble when rolled between the fingers. The critical stage of wilting was considered as having been attained, as in the case of Norway spruce, with the development of pronounced epidermal wrinkling, just at the beginning of twisting. At this stage the seedlings recovered if the bed was watered. The lethal stage occurred after twisting began but before brittleness developed.

Decreasing Water-Content in Norway Pine Seedlings as Drying Went on

Data of moisture content of tops and atmometer losses.—In Table XI are given the data on moisture content of tops for the experiments with sand-

TABLE XI. *Water-contents and dry weights of tops of sand-grown Norway pine seedlings at times of successive observations in each experiment, together with corresponding cumulative values of water loss from the white atmometer sphere.*

Exp. no., etc.	Date of observation, (1929)	Total corrected atmometer loss,[1] *Ml.*	Average dry wt. per plant top, *Mg.*	Water content of plant tops		
				Average per top, *Mg.*	Ave. of percentage water: contents based on corresponding dry weights	
					Actual *Per cent.*	Relative to 1st value as unity.
No. 10.	Dec. 6	0	4.9	21.5	442	*1.00*
	8	39	4.9	20.3	419	*0.95*
24-day period,	10	77	5.0	22.5	451	*1.02*
standard	11	93	5.1	21.9	428	*0.97*
watering.	12	107	4.7	20.3	431	*0.97*
	13	119	5.0	20.6	414	0.94
	14	133	4.8	18.4	383	**0.87**
	15	150	5.2	19.2	367	0.83
	16	169	4.9	16.6	334	0.76
	18	198	5.2	15.8	308	0.70
	22	265	4.8	8.3	145	0.33
	(1930)					
No. 11.	Jan. 15	0	4.5	24.4	542	*1.00*
	17	30	4.6	23.9	521	*0.96*
24-day period,	19	66	4.9	24.1	497	0.92
standard	21	106	4.8	22.9	472	0.87
watering.	23	137	5.6	24.5	436	**0.80**
	24	157	5.8	22.6	390	0.72
	25	182	5.9	21.7	372	0.69
	28	239	5.7	20.8	365	0.68
	31	289	5.7	18.2	329	0.61
	Feb. 4	375	6.0	10.8	174	0.32
No. 12.	Jan. 15	0	4.5	22.9	510	*1.00*
	17	30	4.9	24.2	499	*0.98*
24-day period,	19	66	4.6	22.3	481	0.94
standard	20	88	5.0	23.2	469	0.92
watering.	21	106	5.4	24.9	467	0.92
	23	137	5.0	22.3	443	0.87
	24	157	5.7	22.8	400	**0.78**
	25	182	5.6	21.8	386	0.76
	28	239	5.8	21.9	376	0.74
	31	289	5.7	21.0	366	0.72
	Feb. 4	375	6.4	15.3	237	0.46
No. 13.	Feb. 23	0	4.3	23.0	551	*1.00*
	25	37	4.7	23.8	512	0.93
24-day period,	26	70	4.8	23.0	491	0.89
deficient	27	83	4.9	24.0	492	0.89
watering.	28	105	4.2	24.1	436	**0.79**
	Mar. 1	133	5.2	20.8	397	0.72
	4	187	5.6	16.5	266	0.48
No. 14.	Feb. 13	0	6.1	20.2	336	*1.00*
	16	52	6.6	19.9	306	0.91
55-day period,	18	94	6.6	20.1	295	0.88
standard	22	223	7.3	18.1	259	0.77
watering.	23	247	6.5	17.5	251	0.75
	24	261	7.3	16.7	236	**0.70**
	25	284	7.0	12.8	192	0.57
	26	317	7.3	11.1	148	0.44
	28	352	6.9	4.8	68	0.20

[1] From white sphere, since first observation.

grown Norway pine seedlings, along with the corresponding records of water loss from the white atmometer sphere. Computations were performed just as in the experiments with the Norway spruce and Table XI is arranged like Table V.

The dry weights of Norway pine seedlings.—While the Norway spruce seedlings generally showed no significant increase in average dry weight per seedling top during the period of the experiments (*i. e.,* after watering of the beds had been discontinued), the Norway pine seedlings showed a significant increase in four of the five experiments. Experiment 10 is the exceptional one; for a span of 17 days the average dry-weight per top varies only between 4.7 and 5.2 mg.

Experiments 11, 12 and 13 all show a considerable increase in average dry weight throughout the experiment period. The average dry weight for the first day of experiment 11 is 4.5 mg. and for the last day it is 6.0 mg., or 33 per cent greater. The rise was remarkably gradual in this case; the average for each two successive values is regularly greater than that for the preceding pair. Experiments 12 and 13 are similar to Experiment 11 in this respect. The actual increase amounts to 42 per cent in the case of Experiment 12. In spite of the fact that the drying period was much shorter in Experiment 13 than in Experiments 11 and 12, there was still an increase of 30 per cent in average dry weight in Experiment 13. Every value in the series is greater than the preceding one. In Experiment 14 the dry-weight increase is not so apparent because the last value is exceptionally low. Neglecting that value, however, there is an increase from 6.1 to 7.3 mg., or 20 per cent.

It appears that the Norway pine seedlings used in these experiments were generally in a phase of development where increase in non-water content had recently begun and that this change continued throughout the drought period, to the end of the experiment. Dry weight decreases during the germination of the seed and the early phases of seedling development. This is true for green plants in general. Eventually there comes a time, after the plantlet has emerged from the soil, when the photosynthetic process more than makes up for respiratory loss, at which time the non-water content of the seedling begins to increase. Whether the dry weight decreases, increases, or is maintained for a number of days depends upon how advanced the organism is and upon light and carbon-dioxide conditions. In this respect it seems that the Norway spruce seedlings of this study were generally not so far advanced as those of Norway pine. It is interesting to note, however, that the Norway pine seedlings generally had somewhat lower dry weights than were shown by Norway spruce seedlings of similar culture and of about the same age. This is not to be regarded as a generalization, for some set of culture conditions sufficiently different from those employed in this study might establish quite different relations between these species. Another observation that may be interesting is that the lowest average dry weights for Norway pine seedlings

were for those that had been grown with deficient or barely adequate water supply (Exp. 13), which is also true of the experiments with Norway spruce, as has been mentioned.

Reverting to the general increase in average dry weight of the Norway pine seedlings during the period without watering, it is remarkable that this increase continued long after the plants had attained what is here termed the critical stage of wilting. In Experiments 11, 12 and 13 there seems to be no doubt that average dry weight was still increasing between the next to the last observation and the last. At the time of critical wilting these plants had average dry weights of 5.6, 5.7 and 4.2 mg., and in the succeeding 12 or 15 days these values increased to 6.0, 6.4 and 5.6 mg., respectively. Before the last observation these seedlings were apparently dead; they had surely passed the stage where they might recover if the bed were watered, and yet the dry weight of their tops continued to increase. This relation would make an interesting subject for special study. At any rate it is worthy of remark in passing.

Early-morning water contents of healthy Norway pine seedlings, before drought effects were apparent.—The regular decrease in average water content of seedling tops began much more promptly in the experiments with Norway pine than in the experiments with Norway spruce. The first relative average water-content percentage was again taken as 1.00 in Experiments 10—14 and it is remarkable that in only one instance (Dec. 10, Exp. 10) did any subsequent relative value have a magnitude as great as unity. As in Table V, so also in Table XI (last column), all relative percentage values above 0.94 are shown in italics, to set off that portion of each series that may be considered as representing seedlings that were still in health. That period is seen to have been 12 days in Experiment 10, but it was only 3 days in Experiments 11 and 12 and only 1 day in Experiments 13 and 14. In general, it was much shorter with Norway pine than with Norway spruce.

For Experiment 10, in which the average dry weight of tops showed no clear evidence of increase during the period without watering, the decrease in average water-content percentage is explained by the corresponding decrease in average water-content per seedling top. The percentage, being a ratio value, becomes smaller as its numerator (average water content per top) is smaller, and its denominator varies only irregularly in this instance. Therefore the water-content percentages and their relative values follow the decrease in average water-content per top, as in the case of the experiments with Norway spruce.

For Experiments 11—14 water-content percentages on the dry-weight basis decreased throughout the experiment period partly because of lowered average water content per top and partly because of increased dry weight, in a manner similar to that shown by the Norway spruce seedlings that were kept watered for 60, 68 or 97 days after they appeared above the soil. Consequently

the water-content percentage and its relative value decrease for Experiments 11—14 more rapidly than the average water content decreases and also more rapidly than the average dry weight increases. It may be noted that the influence of increasing average dry weight on the magnitude of the percentage ratio is generally greater than is the influence of decreasing average water content per top. Further analysis of this interesting relation may be made from the data given in Table XI if and when such analysis is desired.

The processes that resulted in lowered water-content percentages were occurring even before the water was cut off. It cannot, therefore, be said that the drying out of the soil and the consequent decrease of its water-supplying power were wholly responsible for decrease in water content of the seedlings but merely that they accelerated to a pathological extent a series of changes that were in progress before the soil environment became unfavorable to health.

Turning to the water-content percentages that are taken as having the relative value of 1.00 in these Norway pine experiments (the first value for each experiment), it is interesting to compare their magnitudes with the magnitudes of the corresponding percentages for Norway spruce. These values are assembled in Table XII.

TABLE XII. *Comparison of water percentages of seedlings.*

Age of seedlings and culture treatment	Average water content; percentage of dry weight	
	Norway spruce, %	Norway pine
	Per cent.	*Per cent.*
24 day; standard watering.....	383, 416, 411	442, 542, 510
24 day; deficient watering.....	445	551
55 day; standard watering.....	...	336
60–68 day; standard watering.....	219, 216	...

The Norway pine graphs of water-content of tops and their critical values.—Figs. 11—15 present graphs of the relative values of water-content percentages for the five Norway pine experiments, arranged like the graphs for Norway spruce in Figs. 2—10. Soil-point data are not shown in these figures for Norway pine. The average water-content percentages that correspond to the critical stage of wilting in these experiments with Norway pine are shown below, with the corresponding critical values from the Norway spruce experiments.

It may be seen that the critical relative percentages for the 24-day seedlings with standard or deficient watering have a range from 0.78 to 0.87 for Norway pine, almost exactly the same as for Norway spruce (0.80 to 0.89). For this class of seedlings, for both species, critical wilting occurred when

the water-content percentage had decreased to about 80 per cent (pine) or 85 per cent (spruce) of its value when watering was discontinued. For the 55-day pine seedlings the critical relative water-content value appears to have been significantly lower (0.70) than the corresponding value for the 24-day seedlings. This is not true for the 60- to 68-day spruce seedlings, for which the critical values are about the same as those for the corresponding 24-day seedlings.

TABLE XIII. *Critical water-content percentages of seedlings.*

Age of seedlings and culture treatment	Critical ave. water-content percentage on basis of dry wt.			
	Norway spruce		Norway pine	
	Absolute	Relative	Absolute	Relative
	Per cent.		*Per cent.*	
24 da., standard watering ...	340	0.89	383	0.87
	353	0.85	436	0.80
	327	0.80	400	0.78
24 da., deficient watering....	338	0.86	436	0.79
55 da., standard watering ...	...	....	236	0.70
60-68 da., standard watering.	190	0.87	...	....
	185	0.86	...	....

The graphs for Experiments 10, 13 and 14 (Figs. 11, 14, 15) each slope downward regularly beyond the point representing the critical water-content percentage and no significant change in the slope of the graph is shown. For Experiments 11 and 12 (Figs. 12, 13), however, the slope of each graph decreases after the critical point has been passed. For a considerable period after the critical degree of wilting had occurred these pine seedlings maintained nearly the same water-content percentage. Beyond this gently sloping portion of the graph the slope is accelerated and again takes a direction about like the slope of the portion at the left of the critical point. It may be that the above-mentioned temporary retardation in the decrease of the water-content percentage of tops represents for Norway pine the phenomenon that was brought out by several of the graphs for Norway spruce for about the same regions. Whatever may be the explanation of the period of nearly maintained water-content percentage in these two experiments with pine, it is evident in only these two.

CRITICAL INITIAL WATER-SUPPLYING POWER OF THE SOIL FOR THE NORWAY PINE BEDS

The soil-point readings taken at the advent of the critical wilting stage in the Norway pine seedlings gave results in every way consistent with those obtained in the experiments on Norway spruce. These critical indices of the

initial water-supplying power of the soil are shown in Table XIV. Each value represents the average of four or five soil-point readings. The corresponding values for Norway spruce are also shown.

TABLE XIV. *Critical indices of water supplying power of soil.*

Age of seedlings and culture treatment	Initial water-supplying power of soil at occurrence of the critical stage of wilting.	
	Norway spruce	Norway pine
	Mg.	*Mg.*
24 da., standard watering.....	26	18
	27	20
	26	19
24 da., deficient watering.....	20	12
24 da., excessive watering.....	59	—
	58	—
55 da., standard watering.....	—	11
60 to 68 da., standard watering. ..	20	—
	12	—

As with Norway spruce, the onset of the critical stage of wilting in the pine seedlings occurred with different values of this soil index, according to the soil moisture conditions under which the plants had grown and according to the age of the plants. For the 24-day seedlings the critical soil-moisture index is markedly lower (about 19 mg.) for the Norway pine seedlings than for the Norway spruce seedlings (about 27 mg.), and this relation holds for the other groups. For both species the critical soil-moisture index is lower for the seedlings that had had deficient water supply than for those of the same age with standard watering. Also, for both species the critical index is lower for the older seedlings with standard watering than for the 24-day cultures with like treatment. For both species the three experiments with 24-day beds watered in the regular way gave remarkably similar soil-point readings for the critical water-supplying power. This observation furnishes an illustration of the highly consistent results that may be secured by means of soil points in a study of this sort.

Results With Additional Species

General remarks.—Besides the 14 experiments for which results have been presented above, one regular experiment was carried out with seedlings of each of the following additional species: white spruce, northern white cedar, shortleaf pine, slash pine, western yellow pine, western white pine, Douglas fir, lowland white fir, western red cedar, and western hemlock. The numerical results of these ten experiments are presented in Table XV, which is in the same style as Tables V and XI.

TABLE XV. *Water-contents and dry weights of tops of sand-grown seedlings of ten species of coniferous trees at times of successive observations in each experiment, together with corresponding cumulative values of water loss from the white atmometer sphere. (In every case the seedlings were about 24 days old and had had standard watering.)*

Exp. no. and species	Date of observation 1929-1930	Total corrected atmometer loss,[1] *Ml.*	Average dry wt. per plant top, *Mg.*	Water content of plant tops		
				Average per top, *Mg.*	Ave. of water-content percentages based on corresponding dry weights	
					Actual *Per cent.*	Relative to 1st value as unity.
Exp. 15.	Dec. 10	0	3.5	15.1	427	*1.00*
	12	30	3.3	14.4	430	*1.01*
White spruce.	14	56	3.5	14.4	418	*0.98*
	15	73	3.4	13.6	395	0.92
	16	92	3.6	13.1	364	**0.85**
	17	107	3.6	11.8	330	0.77
	18	121	3.6	9.6	264	0.62
	19	131	3.5	4.8	139	0.33
	21	166	3.4	3.2	094	0.22
Exp. 16.	Dec. 12	0	1.6	6.0	388	*1.00*
	15	43	1.7	6.6	402	*1.04*
Northern white cedar.	16	62	1.6	6.6	399	*1.03*
	17	77	1.5	6.4	402	*1.04*
	18	91	1.6	5.4	322	**0.83**
	19	101	1.4	4.5	308	0.79
	20	113	1.4	3.5	249	0.64
Exp. 17.	Dec. 9	0	6.4	34.5	514	*1.00*
	11	34	6.5	32.7	514	*1.00*
Shortleaf pine.	13	60	7.0	31.6	479	0.93
	14	74	6.7	32.0	476	0.93
	15	91	8.1	33.1	486	0.95
	16	110	6.2	30.9	487	0.95
	17	125	7.6	35.4	469	0.91
	18	139	7.8	30.0	399	**0.78**
Exp. 18.	Dec. 10	0	16.9	89.8	537	*1.00*
	12	30	14.6	82.0	542	*1.01*
Slash pine.	14	56	16.6	85.9	529	*0.99*
	15	73	17.8	91.8	516	*0.96*
	16	92	15.9	72.4	516	*0.96*
	17	107	15.0	78.2	526	*0.98*
	18	121	12.9	39.9	318	**0.59**
Exp. 19.	Dec. 12	0	17.7	92.0	528	*1.00*
	17	77	17.6	92.3	528	*1.00*
Western yellow pine.	18	91	16.7	87.2	524	*0.99*
	19	101	17.8	68.0	412	**0.79**
	21	136	18.8	49.7	267	0.51
	(1930)					
Exp. 20.	Feb. 13	0	9.0	41.4	457	*1.00*
	16	52	9.9	42.1	425	0.93
Western white pine.	18	94	10.5	40.9	391	0.86
	20	152	11.1	39.8	359	0.79
	21	188	12.6	37.3	293	**0.64**

[1] From white sphere, since first observation.

TABLE XV *(continued).*

Exp. no., and species	Date of observation 1929–1930	Total corrected atmometer loss[1]	Average dry wt. per plant top.	Water content of plant tops		
				Average per top.	Ave. of water-content percentages based on corresponding dry weights	
					Actual	Relative to 1st value as unity.
		Ml.	*Mg.*	*Mg.*	*Per cent.*	
	(1929)					
Exp. 21.	Dec. 15	0	6.4	36.8	574	*1.00*
	17	34	6.5	37.1	567	*0.99*
Douglas fir (Pacific).	19	58	6.9	37.3	556	*0.97*
	20	70	6.2	37.4	603	*1.05*
	21	93	7.6	36.1	476	**0.83**
	22	115	7.6	35.1	466	0.81
	(1930)					
Exp. 22.	Mar. 1	0	11.9	69.3	594	*1.00*
	4	54	12.3	68.3	578	*0.97*
Lowland white fir.	6	100	11.9	61.0	654	*0.95*
	7	126	12.4	54.3	448	**0.75**
	10	207	14.1	42.4	307	0.52
	13	260	12.9	41.7	322	0.54
Exp. 23.	Feb. 20	0	1.4	7.2	508	*1.00*
	22	71	1.4	6.4	466	0.92
Western red cedar.	23	95	1.4	6.1	418	0.82
	24	109	1.6	6.1	405	0.80
	25	132	1.8	4.1	140	**0.28**
	26	165	1.9	0.5	026	0.05
	28	200	1.6	0.1	010	0.02
Exp. 24.	Mar. 7	0	1.0	5.1	531	*1.00*
	9	56	1.0	5.0	519	0.98
Western hemlock.	10	81	1.0	4.8	512	0.96
	11	105	1.0	2.6	256	**0.48**
	13	134	1.0	1.9	187	0.35

In all these experiments the beds received standard watering, which was discontinued about 24 days after the plants emerged from the soil. Because of scanty germination, however, some of these experiments were carried out with seedlings of somewhat more varied age than was regular and samples of between five and six seedlings each, instead of the regular ten, were used. The experiments with white spruce, northern white cedar, shortleaf pine, and western hemlock (Exps. 15, 16, 17 and 24) were quite regular in all ways but the results of the others here considered are perhaps not quite so reliable in some respects as are those with the species just mentioned. Since there is but a single experiment for each of these ten additional species, however, the results must be regarded as no more than indicative or suggestive at best.

Decreasing Water-Content of Tops as Drying Went On

Appearance of seedlings of the ten supplementary species at the stage of critical wilting.—The critical stage of seedling wilting for each of the 10 supplementary forms with which only single experiments were performed was considered as attained when the plantlets had become clearly injured by inadequate water supply but before the cotyledons had become brittle through drying. At this stage the morphological characteristics in the case of white spruce, shortleaf pine, western yellow pine, western white pine, and Douglas fir were very similar to those for Norway spruce and Norway pine with about the same degree of drought injury. Seedlings of lowland white fir showed at this stage wrinkling and the beginning of twisting in the cotyledons and the upper region of the hypocotyl was somewhat bent as if nutation were occurring or drooping had set in. As slash pine seedlings came to the critical stage their cotyledons exhibited marked drooping, hanging obliquely downward within about 30° of the still vertical hypocotyl. Critically wilted seedlings of northern white cedar, red cedar, and western hemlock had markedly wrinkled cotyledons and wilting advanced with great rapidity in these cases; these seedlings showed no visible effects of drought on the morning of the day when the critical stage was to be attained and wilting had definitely reached the critical stage by nightfall. In the case of the two cedars, when this wilting stage was attained the middle part of each comparatively broad cotyledon had become definitely thinner than the marginal portion, through partial collapse of the underlying tissues. Thus these cotyledons showed raised margins and depressed middle regions when viewed either from above or from below. As has been said, it is practically impossible to detect by simple ocular observation the attainment of any definite stage of wilting in the seedling conifers with which this study deals and these notes on the appearance of critically wilted plantlets are consequently much less definite than would be desirable if more satisfactory descriptions were possible.

The dry weights.—White spruce, northern white cedar, slash pine, western yellow pine and western hemlock resembled Norway spruce in showing no significant increase in the dry weight of seedling tops within the experiment period. The dry weights of the seedlings of shortleaf pine, lowland white fir, and western red cedar may have increased slightly. The experiments with western white pine and Douglas fir showed a steady and unquestionable increase in dry weight. For western white pine the final average dry weight is 40 per cent higher than the initial one and for Douglas fir an average dry-weight increment of 19 per cent is shown.

This question of increase in average dry weight per seedling is important in connection with the interpretation of the decrease in water-content percentage, as has been pointed out. It also furnishes one kind of dynamic criterion by which the physiological maturity of a stand of seedlings may be

estimated. Those seedlings that showed no increase in dry weight during the experiment period would have shown increase if they had been somewhat more advanced in development and those that did show definite increase in dry weight would have shown a higher rate of increase if watering had been maintained somewhat longer.

Early-morning water-contents of healthy seedlings, before drought effects were apparent.—The seedlings of most of the species here considered followed the course of the Norway spruce seedlings in exhibiting a considerable period, after the water supply had been cut off, during which the relative water-content of tops remained above 0.94. For white spruce this period lasted for 5 days (the average duration for Norway spruce), for northern white cedar it continued for 6 days and for shortleaf pine 8 days elapsed during which there was no significant decrease in the water-content percentage, although it is true in this instance that two intermediate values were as low as 0.93. The slash pine seedlings also maintained an average water-content percentage above 0.94 for 8 days; those of western yellow pine, for 7 days; and those of Douglas fir and lowland white fir, for 6 days. The seedlings of western hemlock, which had very shallow root systems, were able to maintain apparent health for 4 days after watering was discontinued. These time periods may be translated into terms of atmometer loss by means of the data given in Table XV. The seedlings of western white pine and western red cedar showed relative average water-content percentages below 0.94 at the time of the second observation and the decrease in this index value was scarcely accelerated at the onset of the critical stage of wilting.

Water-contents of tops at the critical stage of wilting.—The actual and relative water-content percentages of tops (on basis of dry weight) that corresponded to the occurrence of the critical stage are shown in Table XVI.

The unusually low water-contents for western red cedar and western hemlock (Exps. 23 and 24) may have been due to the very limited extent to

TABLE XVI. *Actual and relative water-contents of various conifer seedlings.*

Exp. No.	Species	Critical water-content percentage of tops on basis of dry weight	
		Absolute	Relative to 1st value in series
		Per cent.	
15	White spruce	364	0.85
16	Northern white cedar	322	0.83
17	Shortleaf pine	399	0.78
18	Slash pine	318	0.59
19	Western yellow pine	412	0.79
20	Western white pine	293	0.64
21	Douglas fir	476	0.83
22	Lowland white fir	448	0.75
23	Western red cedar	140	0.28
24	Western hemlock	256	0.48

which the root systems of these seedlings had developed at the time observations began. These had by far the shallowest roots of any of the forms tested. Furthermore, these two experiments were carried out at times of unusually intense evaporation, and drying out proceeded with unusual rapidity. The low water-content percentage for western white pine (Exp. 20) at the occurrence of the critical wilting stage may have been due to inadequate sampling of the stand. In any event, this was the most inadequately sampled of any of the species tested. Of the remaining seven experiments in this group, all but Experiment 18 (slash pine) show critical water-content percentages within the same general range as was shown for Norway spruce and Norway pine.

Critical Initial Water-Supplying Powers of the Soil for the Supplementary Experiments

The average soil-point readings corresponding to the critical stage of wilting for the ten supplementary species are shown in Table XVII. The readings from the 24-day experiments with standard watering for Norway spruce and Norway pine are also included in the list, each of these values being the average from three experiments. The values are arranged in the order of increasing magnitude.

Table. XVII. *Critical soil point readings.*

Exp. No.	Species	Critical soil-point reading
		Mg.
19	Western yellow pine	11
17	Shortleaf pine	12
18	Slash pine	13
21	Douglas fir	14
22	Lowland white fir	14
23	Western red cedar	14
10, 11, 12	Norway pine	19
20	Western white pine	20
16	Northern white cedar	22
24	Western hemlock	25
2, 3, 6	Norway spruce	26
15	White spruce	30

The twelve species appear to fall into three groups according to these critical soil-point values: (1) those with critical values from 11 to 14, (2) those with values from 19 to 22 and (3) those with values from 25 to 30. This classification may be suggestive in connection with the relative drought resistance of seedlings of the several species, but it is based on single experiments only, excepting for Norway spruce and Norway pine, and in any event this arrangement naturally refers only to the lots of seed used in this study, to the general technique employed in the writer's experiments, and to the climatic conditions of these experiments.

SUMMARY AND CONCLUSIONS

The studies here reported were made in the Laboratory of Plant Physiology of the Johns Hopkins University during 1929 and 1930. Sand beds of seedling coniferous trees of 12 species were maintained with good moisture conditions in a greenhouse room for about 24 days after the plantlets had emerged from the soil, and for longer periods in some instances. Most of the beds were watered in the ordinary way (standard watering) but in a few instances watering was either excessive or deficient. Deficient watering implies a degree of watering just adequate to maintain health. The beds with excessive watering were kept considerably wetter than those with standard watering. After the growing period the cultures were allowed to dry out without further watering and the progress of wilting and drying was followed by means of frequent ocular observations on the plants as well as by means of average water-content measurements made from day to day on the tops of representative 10-plant samples, the roots of the sample seedlings being discarded. The water-content values were expressed as percentages on the basis of dry weight and these percentages for each experiment were also expressed as a series of relative values, considering as 1.00 the average percentage given by the first sample of tops, taken on the day following the cessation of watering. The average dry weight per seedling increased during the period of drying out for some species and remained without significant change for other species. Data on average dry weight per seedling and on average actual water-content per seedling are presented and discussed, as well as the moisture-content percentages.

Nine experiments were performed with seedlings of Norway spruce (*Picea excelsa* Karst.) and five experiments were on seedlings of Norway pine (*Pinus resinosa* Ait.). Only a single experiment was performed with each of the following forms: white spruce (*Picea glauca* (Moench) Voss.), northern white cedar (*Thuja occidentalis* L.), western red cedar (*T. plicata* D. Don.), shortleaf pine (*Pinus echinata* Mill.), slash pine (*P. caribaea* Morelet), western yellow pine (*P. ponderosa* Laws), western white pine (*P. monticola* D. Don.), Douglas fir (*Pseudotsuga taxifolia* Britt.), lowland white fir (*Abies grandis* Lindl.) and western hemlock (*Tsuga heterophylla* Sarg.).

Two observational stages of wilting and drying of the leaves and stems were recognized: a critical stage of wilting, probably corresponding to the onset of what has been called permanent wilting, and a stage of withering, at which the leaves and stems became brittle. Permanent wilting is taken to mean that phase of wilting in which the seedlings could not recover if transpiration were stopped but could recover promptly if the soil were adequately watered. The critical stage of wilting, at which the plants were still alive, was marked by considerable wrinkling of hypocotyl and cotlyedons and the beginning of a characteristic twisting of the cotyledon tips.

The diurnal fluctuation in plant moisture content, which has been described for other plants by several experimenters, was specially studied for Norway spruce. Because of this fluctuation all samples for measurement of the water contents of seedling tops were taken just before sunrise, before the daytime lowering of water content had set in.

When the first critical stage of wilting (approximately the beginning of the phase of permanent wilting) was seen to be approaching, or when that stage was judged to have been attained, measurements of soil-moisture conditions were made and in a number of experiments these were repeated at frequent intervals until the second critical stage of wilting (brittleness of leaves) had been reached. Soil-moisture measurements were made by means of standardized Livingston soil points, several simultaneous readings being taken, with different instruments, at each observation. The results show how the initial water-supplying power of the soil decreased as the beds dried out and the critical wilting stage was approached and passed. These soil-point readings all refer to an exposure of the instrument for one hour at a depth of 3—5 cm. below the surface of the bed. They are given in terms of milligrams of absorption per soil point and refer to an absorption area of about 12 sq. cm. A special series of tests showed the relation between soil-point reading and soil-moisture content for the upper 4 cm. of soil in a bed like those used for the seedlings. By means of a table based on the results of these tests the supplying-power values may be approximately translated into water-content values.

Records were kept of the climatic conditions of the greenhouse room in which the experiments were performed and the duration factor for the experiments was expressed in terms of total water loss from a standardized Livingston porous-porcelain atmometer sphere as well as in terms of time. Each observation of plant moisture and of soil moisture is shown as having occurred when the white atmometer sphere had lost a specified amount of water since the day following the cessation of watering of the seedling bed. But the corresponding number of days is also given in every case. The atmometric measure is an integration of time and the varying intensity of evaporation conditions and it is consequently more satisfactory than time alone in studies of this sort, when climatic conditions fluctuate in any experiment period.

It was found that the critical stage of wilting, as judged by ocular observation, corresponded fairly closely to a certain amount of decrease in the percentage representing the water-content of tops. Thus the average water-content percentage (on the basis of the corresponding dry weight of tops) furnished a more satisfactory criterion for detecting the onset of the critical stage of wilting than could be had by ocular observation. For the experiments with Norway spruce and Norway pine seedlings the attainment of the critical stage of wilting generally occurred when the average water-content

percentage had decreased by about 15 or 20 per cent of the corresponding value for the healthy plants before drought influence set in. The single experiments with the other 10 forms suggest that this critical percentage may be expected to vary according to species, but this is no more than a suggestion. It is also suggested that the soil-moisture conditions that prevailed during the growth period may have exerted some influence on the extent to which the water-content percentage had decreased at the onset of the critical stage of wilting. Considering the water-content percentage for healthy seedlings as 1.00, the corresponding percentage for the attainment of critical wilting ranged between 0.76 and 0.89 for all experiments with Norway spruce seedlings, between 0.70 and 0.87 for all experiments with Norway pine seedlings and between 0.28 (western red cedar) and 0.85 (white spruce) for the ten single experiments with other species.

Experiments with seedlings more than 24 days old (since emerging from the soil) indicated that the average dry weight per seedling top in health increased with advancing development while the corresponding average water-content per top decreased. The water-content percentage for healthy seedlings therefore decreased markedly as the seedlings became older and the same is true for seedlings subjected to prolonged drought leading to the critical stage of wilting.

Graphs are presented to show the manner in which the water-content percentage decreased throughout the experiment period. In some cases the rate of this decrease was temporarily retarded shortly after the critical wilting stage had been passed. After this temporary retardation the rate of decrease in water-content percentage became more rapid and the seedling tops soon became brittle. The temporary retardation may correspond to the general rupture of tensile water columns and to the onset of death. It appears to have occurred when the water-content percentage had decreased by about 25 per cent of its original value for the day after the last watering.

The results obtained with soil points were remarkably consistent and satisfactory. The soil-point averages, showing the initial water-supplying power of the soil (at the 3—5 cm. depth) when the critical stage of wilting was reached in the plantlets, ranged between 11 mg. (55-day Norway pine seedlings and 24-day western yellow pine seedlings, both grown with standard watering) and 59 mg. (24-day Norway spruce seedlings grown with excessive watering). The three Norway spruce experiments on 24-day seedlings grown with standard watering gave soil-point averages of 26 mg., 27 mg., 26 mg. and the three Norway pine experiments gave corresponding averages of 18 mg., 20 mg., 19 mg. It consequently appears that the critical water-supplying power of the soil for the 3—5 cm. depth was significantly lower for the Norway pine seedlings. Older seedlings, with longer roots, did not attain the critical wilting stage until the initial water-supplying power of the soil at the 3—5 cm. depth had decreased to still lower values. On the other hand,

excessively watered 24-day seedlings of Norway spruce reached the critical wilting stage when the water-supplying power of the soil at the standard depth had decreased only to 58 mg. Deficiently watered 24-day seedlings of Norway spruce and Norway pine did not reach the critical stage until the soil-point index had decreased to 20 mg. (spruce) or 12 mg. (pine). For the single experiments with 24-day seedlings of the eight additional species, all grown with standard watering, the critical soil-point index ranged between 11 mg. (western yellow pine) and 30 mg. (white spruce).

To facilitate the interpretation of these critical soil-moisture indices it may be added, for example, that a soil-point reading of 24 mg. represents a water-supplying power of about 2 mg. for a cross-sectional area of 1 sq. cm., for the first hour. The insertion of the soil point compresses the soil considerably and the readings are consequently always somewhat too high to represent the undisturbed soil at the given depth. We may say that the 24-day Norway pine seedlings grown with standard watering did not attain the wilting stage taken to represent the onset of permanent wilting until the soil of the bed, at the 3—5-cm. depth, had become so dry as to be unable to supply water to 1 sq. cm. of absorbing root surface at a rate greater than 2 mg. per hour for the first hour of capillary contact with the advancing roots. At this stage of drying out, the soil of the bed at a depth range greater than 3—5 cm. must, of course, have had a higher supplying power than that just mentioned and at a depth range less than 3—5 cm. the supplying power must have been still lower than 2 mg. per hour. An initial water-supplying power of 2 mg. per square centimeter (24 mg. per soil point) is about one-fourth as great as the supplying power necessary to maintain growth in white clover and Kentucky blue-grass on a Baltimore lawn in summer, according to Livingston's ('28) estimate, which was based on measurements and observations made by Wilson ('27). Livingston says that when the initial water-supplying capacity falls to 4 mg. per square centimeter the grass leaves became dry and tawny within 2 or 3 days.

The most interesting numerical results of this whole study are brought together in summary form in Table XVIII, which is self-explanatory. It will be noted that only three of the nine experiments with Norway spruce seedlings (Exps. 2, 3, 6) represent 24-day seedlings with standard watering while only two represent 24-day seedlings with excessive watering. Three of the five experiments with Norway pine seedlings represent 24-day seedlings with standard watering. For each of the other sets of variables the results were derived from a single experiment. This study was undertaken mainly as an attempt to develop useful methods and as a sort of reconnaisance survey of possibilities, rather than to secure numerical results that might, in themselves, be reliable as representing the several species and the several experimental treatments. Time for a reasonable number of repetitions was lacking. It therefore seemed desirable to make the study broad rather than deep. The

TABLE XVIII. *Summary of critical values for all experiments.*

Species	Kind of watering during growing period.	Approximate age in days[1] of seedlings when watering was discontinued	Exp. No.	Average dry weight per seedling top in Mg.		Average water content per seedling top					Average initial water supplying power of soil[4] at critical wilting; Mg.
						Absolute in Mg.		As percentage on basis of dry weight			
								Actual		Relative, at critical wilting[3]	
				In health[2]	At critical wilting	In health[2]	At critical wilting	In health[2]	At critical wilting		
Norway spruce.....	Standard	24	2	6.3	6.7	24.1	23.1	383	340	0.89	26
			3	5.9	5.9	24.5	21.4	416	353	0.85	27
			6	5.7	5.9	23.1	18.5	411	327	0.80	26
			Ave.	**6.0**	**6.2**	**23.9**	**20.9**	**403**	**340**	**0.85**	**26**
		60	7	7.8	7.6	17.0	14.6	219	190	0.87	20
		68	8	7.9	9.0	17.0	17.0	216	185	0.86	12
		97	9	9.9	9.4	16.1	12.1	166	127	0.76	17
	Excessive	24	1	7.6	7.8	29.9	28.5	396	332	0.84	59
			4	6.0	6.3	23.9	21.8	403	346	0.86	58
			Ave.	**6.8**	**7.1**	**26.9**	**25.2**	**400**	**336**	**0.85**	**59**
	Deficient	24	5	4.7	5.6	20.6	20.0	445	338	0.76	20
Norway pine.....	Standard	24	10	4.9	4.8	21.5	18.4	442	383	0.87	18
			11	4.5	5.6	24.4	24.5	542	436	0.80	20
			12	4.5	5.7	22.9	22.8	510	400	0.78	19
			Ave.	**4.6**	**5.4**	**22.9**	**21.9**	**498**	**406**	**0.82**	**19**
	Deficient	24	13	4.3	4.2	23.0	24.1	551	436	0.79	12
White spruce.....	Standard	24	15	3.5	3.6	15.1	13.1	427	364	0.85	30

[1] Age is reckoned from time seedlings emerged from soil.
[2] "In health" refers to the observation made on the day after the final watering.
[3] The relative percentage value for healthy seedlings (the day after the final watering) is always 1.00.
[4] Water-supplying power always refers to a standard soil point (about 12 sq. cm.), to a depth of 3-5 cm. and to a 1-hour exposure of the instrument.

TABLE XVIII *(continued)*.

Species	Kind of watering during growing period.	Approximate age in days[1] of seedlings when watering was discontinued	Exp. No.	Average dry weight per seedling top in Mg.		Average water content per seedling top					Average initial water supplying power of soil[4] at critical wilting; Mg.
						Absolute in Mg.		As percentage on basis of dry weight			
								Actual		Relative, at critical wilting[3]	
				In health[2]	At critical wilting	In health[2]	At critical wilting	In health[2]	At critical wilting		
Northern white cedar..	Standard	24	16	1.6	1.6	6.0	5.4	388	322	0.83	22
Short leaf pine.....	"	"	17	6.4	7.8	34.5	30.0	514	399	0.78	12
Slash pine.....	"	"	18	16.9	12.9	89.8	39.9	537	318	0.59	13
Western yellow pine...	"	"	19	17.7	17.8	92.0	68.0	528	412	0.79	11
Western white pine...	"	"	20	9.0	12.6	41.4	37.3	457	293	0.64	20
Douglas fir.....	"	"	21	6.4	7.6	36.8	36.1	574	476	0.83	14
Lowland white fir.....	"	"	22	11.9	12.4	69.3	54.3	594	448	0.75	14
Western red cedar....	"	"	23	1.4	1.8	7.2	4.1	508	140	0.28	14
Western hemlock.....	"	"	24	1.0	1.0	5.1	2.6	531	256	0.48	25

results are of course relatively more significant for experiments performed three times or twice than for those performed only once, but in no case is it permissible to place very great reliance on the actual numerical values given. They are only suggestive and indicative at best and they refer only to the experiments from which they were derived. Still, they do show possibilities and probabilities in a general way and they may be useful in planning more thorough experimentation in this important field of seedling physiology and forest ecology.

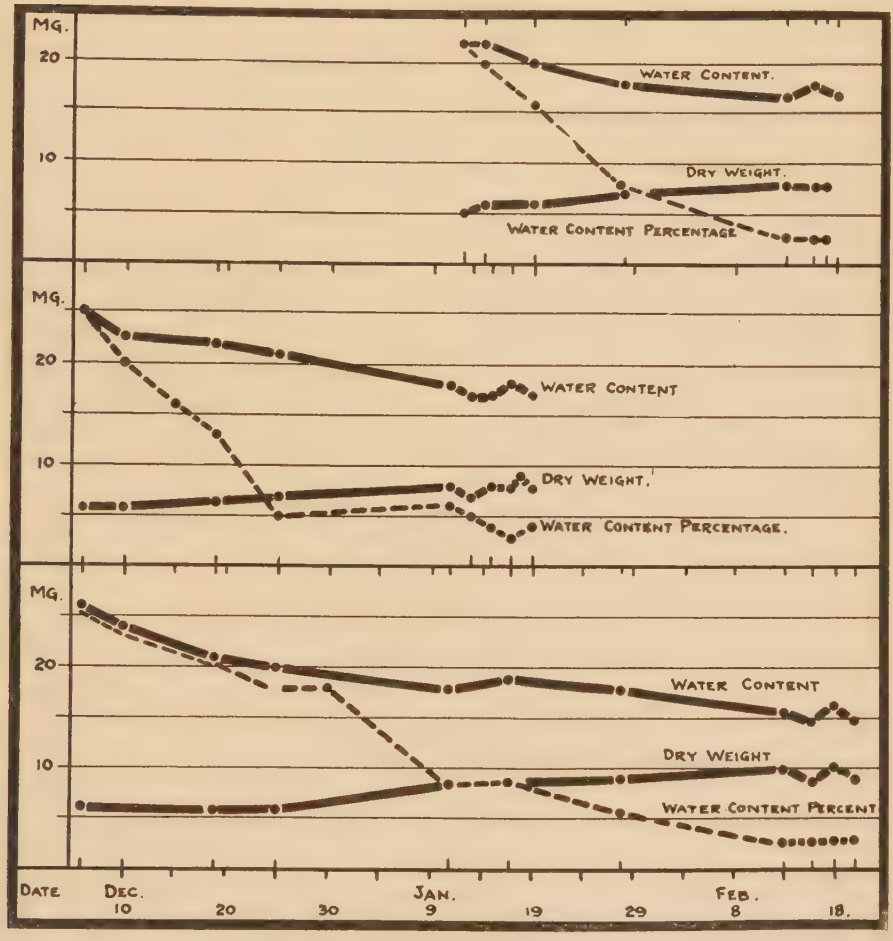

FIG. 1. Graphs showing decrease in average water content of tops and corresponding increase in average dry weight and in the water-content percentage (broken line) as Norway spruce seedlings developed. Data are from Table VIII; the three sets of graphs are for Experiments 7, 8 and 9, respectively.

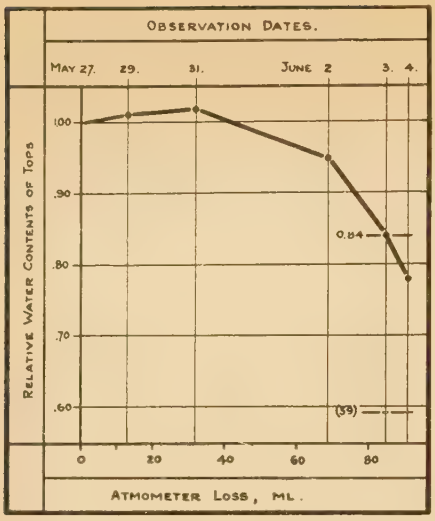

FIG. 2. Graph showing decrease in relative water content of tops of Norway spruce seedlings during Experiment 1. Data are from Table V. Ordinate 0.84 represents the critical stage of wilting and the point below marked 59 (mg.) represents the corresponding average soil-point reading, from Table X.

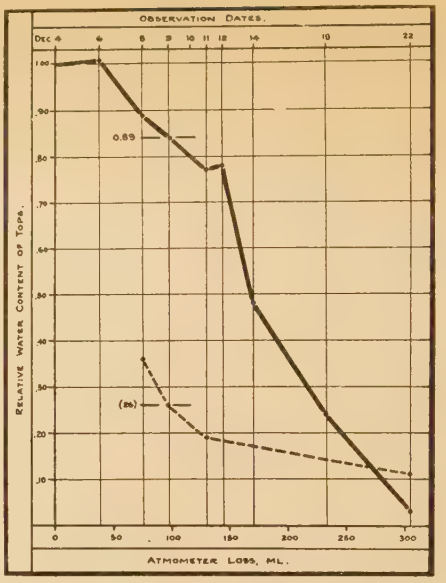

FIG. 3. Graphs showing decrease in relative water content of tops of Norway spruce seedlings during Experiment 2 (continuous line) and the corresponding decrease in average soil-point reading (broken line). Data are from Tables V and X. Ordinates for critical stage of wilting are 0.89 and 26 mg. For the broken-line graph the scale at left is to be read as whole numbers representing milligrams.

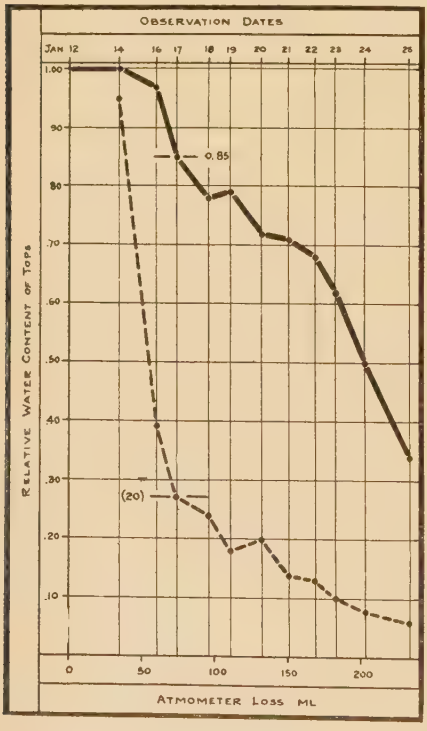

FIG. 4. Graphs as in Fig. 3, but for Experiment 3.

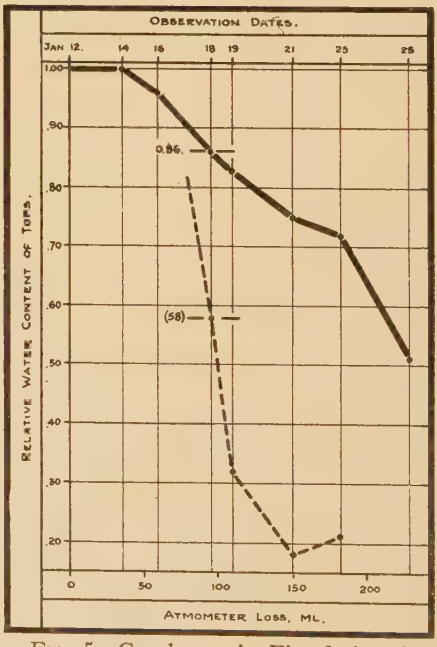

FIG. 5. Graphs as in Fig. 3, but for Experiment 4.

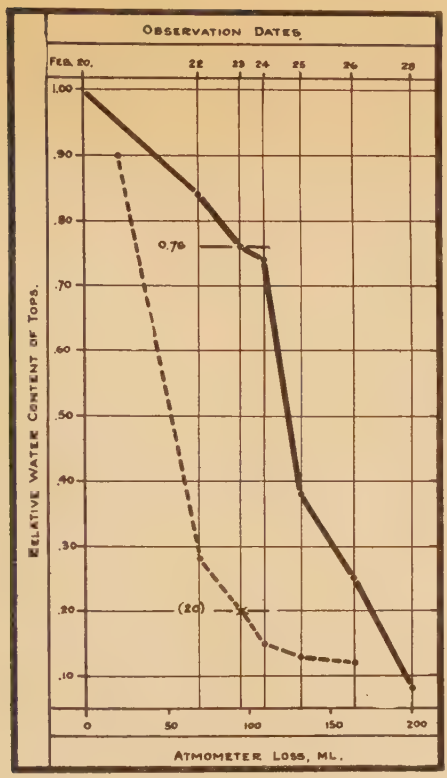

FIG. 6. Graphs as in Fig. 3, but for Experiment 5.

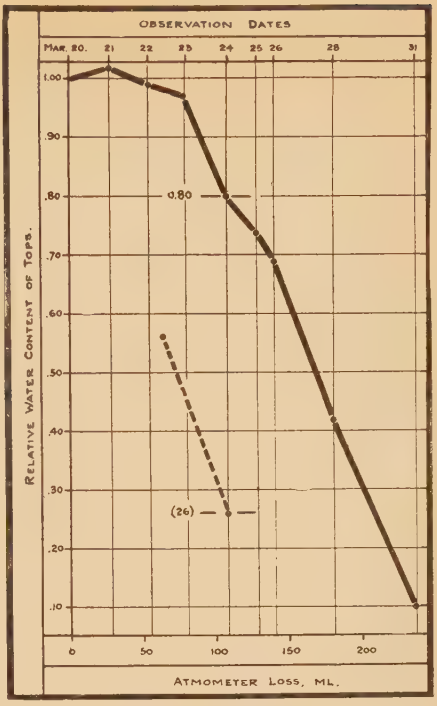

FIG. 7. Graphs as in Fig. 3, but for Experiment 6.

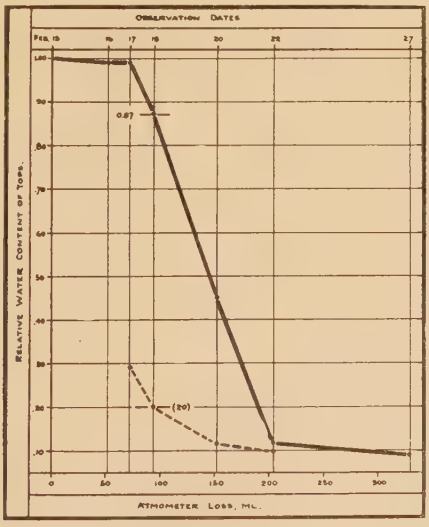

FIG. 8. Graphs as in Fig. 3, but for Experiment 7.

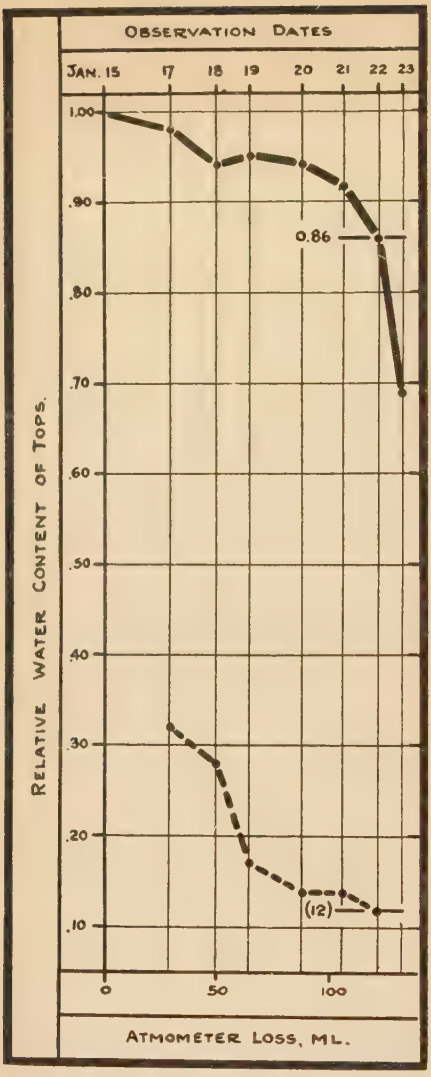

FIG. 9. Graphs as in Fig. 3, but for Experiment 8.

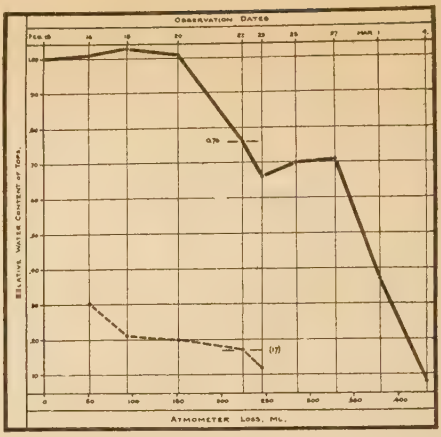

FIG. 10. Graphs as in Fig. 3, but for Experiment 9, with Norway spruce seedlings. Data are from Tables V and X.

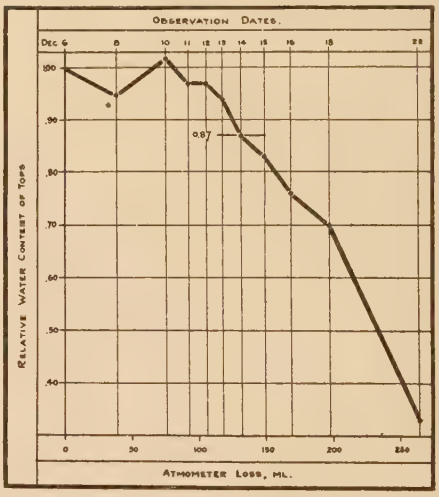

FIG. 11. Graph showing decrease in relative water content of tops of Norway pine seedlings during Experiment 10. Data are from Table XI.

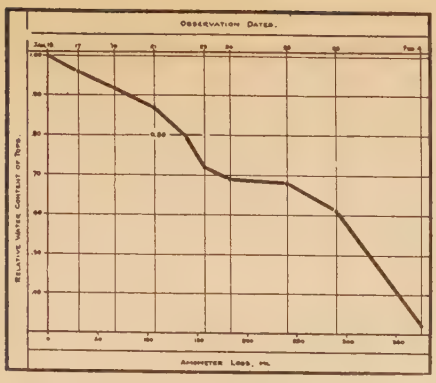

Fig. 12. Graph as in Fig. 11, but for Experiment 11.

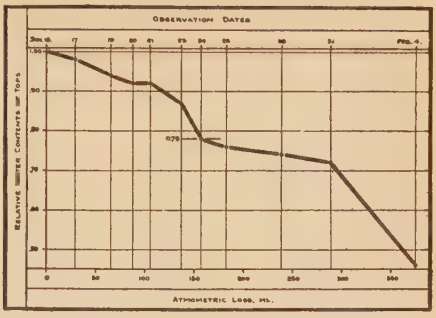

Fig. 13. Graph as in Fig. 11, but for Experiment 12.

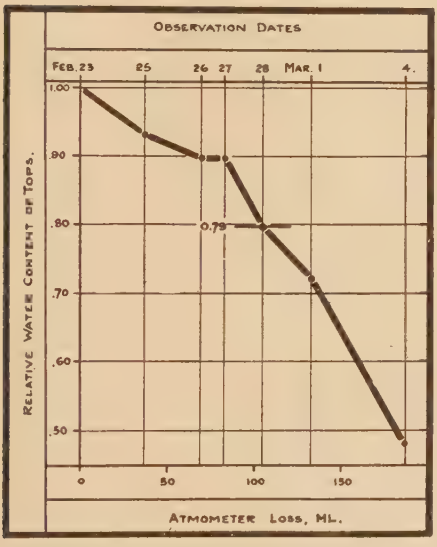

Fig. 14. Graph as in Fig. 11, but for Experiment 13.

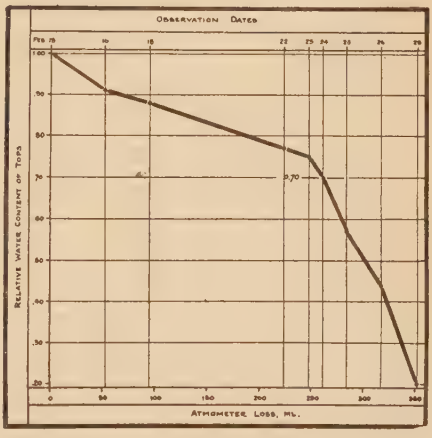

Fig. 15. Graph as in Fig. 11, but for Experiment 14.

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